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A TAXONOMIC REVISION OF *PIERIS* (ERICACEAE)

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THE GENUS *Pieris* comprises seven allopatric and rather distinctive species occurring in both eastern Asia and eastern North America and is closely related to several genera in the Andromedaceae (Ericaceae) (see Stevens, 1971; Judd, 1979). Many of the species are commonly cultivated as ornamentals. I have attempted here to compare the taxa, to interpret their evolutionary relationships, to determine consistent generic and specific concepts, and to develop practical keys for identification.

There are really only two major taxonomic problems involving the genus or taxa within it. The first is to define the limits of the group—that is, to determine the distinctive characters of *Pieris* that separate it from related genera and to determine whether certain species such as *P. nana*, *P. floribunda*, or *P. phillyreifolia* should be segregated as distinct genera (see Nuttall, 1843; Small, 1914, 1933; Makino, 1961; Ohwi, 1965). This problem is discussed in part in Judd (1979). The second is to determine which species can be recognized within the wide range of variation that is found in the eastern Asian plants with subapical placentae and elongated testa cells (i.e., the *Pieris japonica*-*P. formosa* complex).

GENERIC AND INFRAGENERIC RELATIONSHIPS

The genus *Pieris* (Ericaceae subfam. Vaccinioideae tribe Andromedaceae—see Stevens, 1970, 1971; Judd, 1979) is closely related to *Agarista* D. Don (including *Agauria* (DC.) Hooker f.), *Craibiodendron* W. W. Sm., and *Lyonia* Nutt. However, it can easily be differentiated from these genera by a combination of several characteristics. These include: 1) usually unifacial leaf midrib and petiole bundle; 2) coriaceous, serrate to entire, often pseudoverticillate or whorled leaves; 3) inflorescence exposed for some time before flowering, with meiosis occurring in the fall; 4) two more or less alternate

bracteoles; 5) urceolate to elongate-urceolate corollas lacking stomata on the abaxial surface; and 6) usually more or less straight filaments with 7) a pair of stout, minutely papillose spurs at the anther-filament junction; and 8) disintegration tissue on the back of the anther not extending into the spurs. The loculicidal capsules lack the thickened sutures of *Lyonia*, and the seeds do not have the prominent unilateral wing so characteristic of *Craibiodendron*. The multicellular, biseriately-stalked, glandular-headed hairs have only small heads and are thus unlike the swollen-headed glandular hairs or peltate scales of *Lyonia*. All species have an obviously heterogeneous pith except *P. nana* (homogeneous) and *P. cubensis* (heterogeneous, but poorly developed). A more detailed discussion of the evolutionary relationships of the above-mentioned genera is given in Judd (1979).

Pieris nana is very distinctive, differing from the other species of the genus in its low habit, its small, entire, usually whorled leaves, its roughened-papillose filaments, and its anthers with only poorly developed disintegration tissue. Because of these differences, this species has often been placed in the segregate genus *Arcterica*; however, it is here retained within *Pieris* since it resembles the rest of *Pieris* in the many characteristics listed above (see Judd, 1979).

The phylogenetic relationships among the species of *Pieris* have been investigated using the method of Wagner (1961, 1962, 1969, 1980; see also Eldredge & Cracraft, 1980). Sixteen characters were used and assigned generalized (primitive, ancestral, or plesiomorphous) or specialized (advanced, derived, or apomorphic) states. TABLE 1 lists these characters. For each of the characters, each taxon was scored 0 if primitive and 1 if advanced. When two or more states of a given character were considered derived, each was given a lower-case alphabetic superscript (e.g., 1^a, 1^b, 1^c). All taxa are listed in TABLE 2, with the character state values for each. The total divergence index of each taxon was determined by adding the individual character state values of each character together. Then mutual groupings of derived characters were determined (by hand), and the taxa were arranged in sequence according to these groupings. In this process the number of character state reversals was minimized. The taxa were plotted on a concentric graph (FIGURE 1), with the branching points determined by the mutual grouping of derived characters, and the distance by the divergence of each taxon.

The Wagner method, like other cladistic methods, requires numerous assumptions concerning which is the derived and which the ancestral state of each character. The problems and sources of error associated with each step in the procedure are discussed in Judd (1979). The derived state(s) of characters A-F, I-K, and M-P were determined by out-group comparison (using the *Lyonia* group of the Andromedeae as the outgroup—see Stevens, 1970, 1971; Judd, 1979) supported by in-group comparison for character states A, C^a, D, J, K, M, and N. In-group comparison was used in determining the advanced state of G, H, and L. These decisions were made after careful study of the genus and related groups.

FIGURE 1 clearly shows the cladistic distinctness of *Pieris nana* and also indicates that the remaining six species fall into two subgroups. Because of

TABLE 1. Characters used in phylogenetic study* of the species of *Pieris*.

CODE LETTER	CHARACTER	GENERALIZED STATE	SPECIALIZED STATE
A	Habit	Trees or low shrubs	a. \pm Prostrate shrubs (< 10 cm) b. Lianas, climbing within bark
B	Pith	Homogeneous	Heterogeneous
C	Leaf arrangement	Alternate	a. Whorls of 3 b. Pseudoverticillate
D	Leaf length	> 1.5 cm	< 1.5 cm
E	Leaf margin	Entire	At least few teeth present
F	3° veins of leaf	Not prominent (leaves \pm brochidodromous)	Prominent (leaves \pm reticulodromous)
G	Petiole vascular bundle	Unifacial	Bifacial
H	Multicellular hairs	Biseriate-stalked, glandular	Multiseriate-stalked, nonglandular
I	Inflorescence position	Always axillary	Sometimes terminal
J	Flower arrangement	Alternate	Whorls of 3
K	Corolla	Weakly ribbed to unribbed	Strongly ribbed
L	Filament shape	\pm Straight	Geniculate
M	Filament pubescence	Unicellular hairs	a. Smooth b. Roughened-papillose
N	Disintegration tissue	Well developed	Poorly developed to lacking
O	Placentae	Subapical	Central to nearly basal
P	Seed-coat cells	Elongated	\pm Isodiametric

*Wagner method.

the cladistic (and patristic) divergence of *P. nana*, this species is here placed in the monotypic subgenus ARCTERICA; the remaining species are placed within subg. PIERIS, which has been divided into two sections, sect. PIERIS (including *P. japonica*, *P. formosa*, and *P. floribunda*) and sect. PHILLYREOIDES (including *P. phillyreifolia*, *P. cubensis*, and *P. swinhoei*).

The apomorphous character states distinctive of each of these groups are listed below. These characters include some that are unique to the group, indicated by a double asterisk (**), and some that are also found in other groups, indicated by a single asterisk (*). *Pieris nana* (subg. ARCTERICA) is characterized by: A^a (low, prostrate habit)**, C^a (leaves in whorls of

TABLE 2. Character divergence values for each taxon used to construct Wagner Tree.

CHARACTER	TAXA						
	<i>Pieris japonica</i>	<i>Pieris formosa</i>	<i>Pieris floribunda</i>	<i>Pieris phillyreifolia</i>	<i>Pieris cubensis</i>	<i>Pieris swinhoei</i>	<i>Pieris nana</i>
A	0	0	0	1b	0	0	1a
B	1	1	1	1	1/sl.	1	0
C	1b	1b	0	1b	0	1b	1a
D	0	0	0	0	0	0	1
E	1	1	1	1	1	1	0
F	0	1	1	0	0	0	0
G	0	0	0	0	1	0	0
H	0	0	1	0	0	0	0
I	1	1	1	0	0	1	1
J	0	0	0	0	0	0	1
K	0	0	1	0	0	0	0
L	0	0	0	1	0	0	0
M	0	0	0	1a	0	0	1b
N	0	0	0	0	0	0	1
O	0	0	0	1	1	1	1
P	0	0	0	1	1	1	0
TOTAL	4	5	6	8	5	6	8
GEOGRAPHIC LOCATION	EA	EA	NA	NA	WI	EA	EA

Explanation of abbreviations: sl. = only slightly developed, EA = eastern Asia, NA = North America, WI = West Indies.

three)**, D (small leaves)**, I (sometimes terminal inflorescences)*, J (flowers in whorls of three)**, M^b (roughened-papillose filaments)**, N (disintegration tissue poorly developed)**, and O (placenta ± central)*. Subgenus *PIERIS* is characterized by: B (heterogeneous pith, but only poorly developed in *P. cubensis*)** and E (serrate leaves)**. In addition, the group is distinguished by the plesiomorphous characters of an erect, arborescent habit (plants to at least 0.5 m tall), large leaves, and anthers with well-developed disintegration tissue. Section *PIERIS* is characterized by: B (heterogeneous pith)* and I (inflorescences sometimes terminal)*. This group tends to have paniculate inflorescences and has capsules with subapical placentae and strongly elongated seed-coat cells. Finally, sect. *PHILLYREOIDES* is characterized by: B (heterogeneous pith)*, O (central to nearly basal placentae)*, and P (seeds with ± isodiametric testa cells)**. The inflorescences of this group tend to be axillary racemes. The two sections are best differentiated

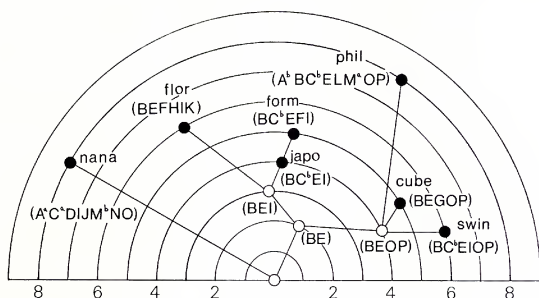


FIGURE 1. Wagner tree for the species of *Pieris*: extant taxa (black circles); hypothetical ancestors showing only derived character states shared by taxa positioned distally in tree (open circles). Derived character states for each taxon listed within parentheses; taxon names abbreviated by first four letters of specific epithet.

on the characters of placenta position and testa-cell shape.

Neither *Pieris phillyreifolia* nor *P. floribunda* has been recognized here as comprising a distinct genus, although each is a very distinct species. *Pieris phillyreifolia* is unique in its climbing habit and in its geniculate and smooth filaments; *P. floribunda*, in its large, multicellular, long-celled hairs and its strongly ribbed corolla. However, these differences are not of a magnitude comparable to those between other genera in the Andromedeae (Judd, 1979). More importantly, the above cladistic study has revealed that *P. phillyreifolia*, in spite of its striking climbing habit, is phylogenetically very close to *P. cubensis*, and that *P. floribunda*, despite its distinctive multicellular hairs, is clearly related to *P. japonica*. The possibility of a close relationship between *P. phillyreifolia*, *P. cubensis*, and *P. swinhoi* was first indicated by Stevens (1969).

DISTRIBUTION AND ECOLOGY

Pieris is likely an ancient genus since it shows an Arcto-Tertiary disjunction pattern between eastern Asia and eastern North America (see discussion in Judd, 1981). The genus is composed of seven species, one of which (*P. nana*) has been placed in the distinctive subgenus ARCTERICA. This species is strictly eastern Asian and occurs in the alpine vegetation of northern Japan, the Kuril Islands, and the southern Kamchatka Peninsula. The species of subg. PIERIS are grouped into two sections, both of which contain species occurring in eastern Asia and eastern North America. These species occur in cool to warm, temperate, broadleaved to coniferous forests on acid soils and are generally sun-loving plants. Section PIERIS contains the closely re-

lated *P. japonica* and *P. formosa*, whose combined distribution extends in an arc from Japan across China and west to Nepal, and the more distantly related *P. floribunda*, which occurs in the southern Appalachians of eastern North America. Section PHILLYREOIDES includes the very rare and little-collected *P. swinhoei* of southeastern China, *P. cubensis* of Cuba (Pinar del Río) and the Isle of Pines, and *P. phillyreifolia* of the southeastern United States Coastal Plain (South Carolina to Florida and west to Mississippi).

All species of the genus are allopatric (MAPS 1-5), and thus no naturally occurring hybrids are known. The process of speciation within the genus seems to have occurred via geographic isolation and subsequent morphological, physiological, and anatomic differentiation, resulting in allopatric pairs of related taxa (e.g., *P. japonica* and *P. formosa*, or *P. cubensis* and *P. phillyreifolia*—see Ehrendorfer, 1976). This process may be at work in the geographic subunits of *P. japonica* (eastern China, Taiwan, Ryukyu Islands, and Japan) since the plants of these regions differ from each other rather inconsistently in a few vegetative and inflorescence characters. It is perhaps significant that among the plants of these geographic subunits of *P. japonica*, the small population on Okinawa is the most distinctive (possibly due to the operation of genetic drift or the founder effect—see Mayr, 1969; Grant, 1971).

TAXONOMIC CRITERIA

HABIT. The species of *Pieris* vary from low, prostrate shrubs only a few centimeters tall (such as *P. nana*) to small trees of 10 m (e.g., *P. formosa* or lianas (*P. phillyreifolia*) that climb within the fibrous bark of *Taxodium*. *Pieris nana* and *P. phillyreifolia* are characteristically rhizomatous, while other species (*P. floribunda*, *P. japonica*, *P. formosa*) lack rhizomes.

As in most members of the Andromedeaceae, the growth of the individual shoot meristem is limited, and increase in height is by a succession of axillary, equivalent, orthotropic shoots (Lems, 1962). All species show Leeuwenburg's Model of growth (Temple, 1975; Hallé, Oldeman, & Tomlinson, 1978) or a slight variation of this architectural pattern. In *Pieris floribunda* the shoot is consistently terminated by the inflorescence; in *P. cubensis* and *P. phillyreifolia* the inflorescences are exclusively axillary, arising from buds near the shoot apex, and the shoot apex aborts. In either case growth continues by means of vegetative shoots arising from buds usually located below the floral buds or the terminal inflorescence. In *P. japonica*, *P. formosa*, *P. swinhoei*, and *P. nana* both terminal and axillary inflorescences may be produced; the axillary inflorescences always arise from buds clustered near the shoot apex. It should be added that rhizomatous species cannot be fitted into Leeuwenburg's Model unless the presence of rhizomes is discounted (i.e., unless only the orthotropic subunits of growth are considered).

With regard to growth architecture, *Pieris phillyreifolia* has diverged from the other species in that it produces orthotropic, scale-bearing shoots that climb within the fibrous bark of *Taxodium ascendens* Brongn. and that give rise at intervals to more or less plagiotropic leafy (and flowering) shoots (see

Lemon & Voegel, 1962; Hallé, Oldeman, & Tomlinson, 1978). However, this species may also form erect shrubs with a growth architecture similar to that of *P. cubensis*, and the climbing habit is likely derived from the rhizomatous-shrubby habit by several specializations involving the horizontal underground rhizome—for example, a change in the rhizomes' geotropic response.

The pith of the young stems is heterogeneous (i.e., with a mixture of large and small cells) in most species but is homogeneous in *Pieris nana* and nearly so in *P. cubensis*.

LEAVES. Leaf arrangement is often a useful taxonomic character within *Pieris*. *Pieris floribunda* and *P. cubensis* have alternate leaves, with the first-formed leaves of the shoot small, scalelike, and quickly deciduous, and those formed later much larger and persistent. *Pieris japonica*, *P. formosa*, *P. phillyreifolia*, and *P. swinhoei* have pseudoverticillate leaves, and *P. nana* usually has leaves in whorls of three.

All species have evergreen, coriaceous leaves with a prominent midvein. The secondary veins are brochidodromous in *Pieris japonica*, *P. swinhoei*, *P. phillyreifolia*, and *P. cubensis*, more or less reticulodromous in *P. floribunda* and *P. formosa*, and hyphodromous to slightly brochidodromous in *P. nana*. *Pieris swinhoei* is distinctive because of its numerous secondary veins that diverge at nearly right angles from the midvein and extend more or less straight toward the edge of the blade, where they interconnect. The leaf shape varies from widely to narrowly ovate, elliptic, or obovate, and the margin from entire to prominently serrulate or serrate. The extent of marginal serration is useful in differentiating *P. japonica* from *P. formosa*, and *P. swinhoei* from *P. cubensis*. *Pieris nana* is the only species with entire leaves. The size of the leaf blade varies from only 3–11 mm in *P. nana* to ca. 18 cm in *P. formosa*, but it also often varies greatly within a species (see especially *P. formosa*). The petiole and midvein vascular bundle is unifacial in most species (FIGURE 2). All species have included secondary veins (FIGURE 2), and the epidermal cells vary from nonlignified (e.g., *P. floribunda* or *P. japonica*) to strongly lignified (e.g., *P. phillyreifolia*). *Pieris cubensis* is distinctive in that it has fibers in the leaf mesophyll (see Stevens, 1970). There is also much variation in the thickness of the ultimate veinlets (FIGURE 2).

INDUMENTUM. The morphology of the unicellular and multicellular hairs is rather uniform within the genus. *Pieris floribunda* is easily distinguished by its large, multicellular, long-celled hairs. All species have multicellular, biserrate-stalked, glandular-headed hairs, as well as unicellular ones.

The distribution of these hair types is, in general, either too uniform or too variable to be of taxonomic value. However, the capsules of *Pieris swinhoei* are densely covered with unicellular hairs, those of the related *P. phillyreifolia* are glabrous, and those of *P. cubensis* are glabrous to only very sparsely pubescent. It is of interest that the capsules of *P. nana* may be glabrous to densely pubescent; those of *P. floribunda*, *P. formosa*, and *P. japonica* are always glabrous.

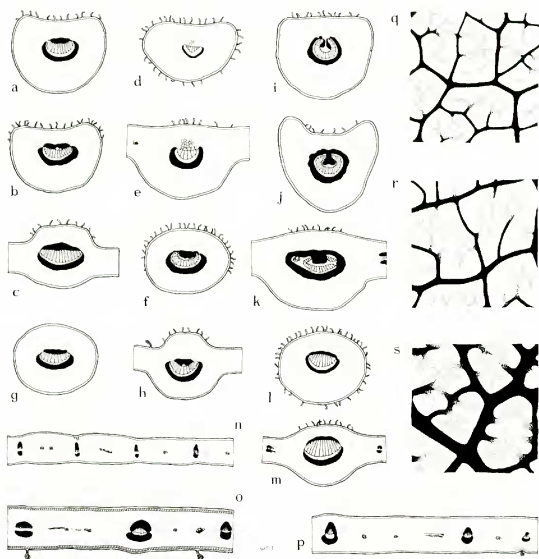


FIGURE 2. Anatomic variation within *Pieris*. a-m, vascular bundle cross sections shown semidiagrammatically; fiber sheath in black, phloem in white, xylem with vertical lines. a-c, *Pieris japonica*, $\times 25$: a, lower petiole; b, upper petiole; c, mid-vein near base of blade. d, e, *P. nana*, $\times 50$: d, mid-petiole; e, near base of blade. f, g, *P. phillyreifolia*, $\times 25$: f, mid-petiole; g, upper petiole. h, *P. swinhoei*, near base of blade, $\times 25$. i-k, *P. cubensis*, $\times 25$: i, lower petiole; j, upper petiole; k, near base of blade. l, m, *P. floribunda*, $\times 25$: l, mid-petiole; m, near base of blade. n-p, cross sections of leaf blades, $\times 50$: n, *P. floribunda*; o, *P. phillyreifolia* (note thick cuticle and lignified epidermis); p, *P. japonica*. q-s, areoles and vein endings (each square = 2.75 mm^2): q, *P. floribunda*; r, *P. japonica*; s, *P. phillyreifolia*.

INFLORESCENCE. The inflorescences in *Pieris* may be terminal or axillary, erect or pendent, and a raceme or a panicle. They are produced in the year preceding flowering—that is, meiosis occurs in the fall, and the essentially mature flowers overwinter. Consequently, most species bloom very early in the spring. The flowers are arranged spirally along the inflorescence axis in all species except *P. nana*, where they are borne in whorls of three. The inflorescence type (i.e., raceme or sparsely to densely branched panicle) and

its degree of erectness vary greatly in *P. formosa* and *P. japonica*. However, since these characteristics are not geographically or ecologically consistent and they intergrade extensively, they can not be used to support the recognition of species such as *P. polita* or *P. taiwanensis*.

FLOWERS. Floral morphology is rather uniform within the genus. The flowers are distributed from near the base to near the apex of the axis and are perfect, pendulous, and fragrant. Each one is articulated with the pedicel, which has a small bract and two lateral, more or less alternate bracteoles. The flowers are five-merous, with coriaceous, elongate-triangular, valvate calyx lobes (which probably protect the other flower parts during the winter). The calyx is usually persistent in fruit, but is often deciduous in *Pieris nana*. The sympetalous corolla is urceolate to cylindrical-urceolate, is sometimes strongly ridged (e.g., in *P. floribunda*), and varies from white to occasionally pink tinged. It is glabrous on both surfaces but is usually slightly papillose toward the mouth. The filaments of the ten stamens are more or less straight except in *P. phillyreifolia*, where they are geniculate. They are always swollen near the base and are smooth in *P. phillyreifolia*, roughened-papillose in *P. nana*, and covered with short to long, unicellular hairs in the remaining species. All species have two stout, minutely papillose spurs at the anther-filament junction. The white disintegration tissue on the back of the anthers does not extend into the spurs. The style is cylindrical and usually slightly swollen near the base. It may be deeply to only slightly sunken into the apex of the ovary.

FRUITS AND SEEDS. The fruit in all species is a loculicidal capsule with unthickened sutures and a persistent central columella on which the slightly bilobed placentae are borne. In sect. **PIERIS** the placentae are borne subapically, while in sect. **PHILLYREOIDES** and subg. **ARCTERICA** they are centrally to nearly basally attached (with respect to the apex of the capsule). The capsule varies from subglobose to ovoid or slightly urceolate.

The seeds are small, brownish, and spindle shaped to cylindrical-ovoid; they may be very slightly winged. The testa cells are of two basic types: elongated in sect. **PIERIS** and *P. nana*, and more or less isodiametric in sect. **PHILLYREOIDES**.

TAXONOMIC TREATMENT

Pieris D. Don, Edinburgh New Philos. Jour. **17**: 159. 1834. TYPE SPECIES: *Pieris formosa* (Wallich) D. Don.

Portuna Nutt. Trans. Am. Philos. Soc. n.s. **8**: 268. 1842. TYPE SPECIES: *Portuna floribunda* (Pursh) Nutt. (= *Pieris floribunda* (Pursh) Bentham & Hooker).

Arctericia Cov. Proc. Washington Acad. **3**: 573. 1901. TYPE SPECIES: *Arctericia nana* (Maxim.) Makino (= *Pieris nana* (Maxim.) Makino).

Ampelothamnus Small, Shrubs Florida, 96. 1913. TYPE SPECIES: *Ampelothamnus phillyreifolius* (W. J. Hooker) Small (= *Pieris phillyreifolia* (W. J. Hooker) DC.).

Evergreen shrubs, trees, or woody vines, occasionally spreading by means of horizontal underground rhizomes, with terete or angled branches and usually gray, longitudinally furrowed bark. Indumentum of unicellular hairs, multicellular, biseriate-stalked hairs with small glandular heads, and sometimes multicellular, multiseriate, long-celled hairs. Buds ovoid, globose, nearly hemispheric, to flattened and \pm triangular in outline, with (2 or) 3 to 6 rounded to acute or acuminate, imbricate scales. Leaves alternate, pseudovercillate, or in whorls of 3, exstipulate, simple, scalelike at base of innovation, petiolate, coriaceous, sparsely covered with multicellular, biseriate-stalked, glandular-headed hairs on both surfaces (also with multicellular, long-celled hairs in *Pieris floribunda*, with unicellular hairs on midvein of adaxial surface; margin entire, obscurely to strongly toothed, or serrulate; venation brochidodromous to reticulodromous, with midvein prominent and 3rd veins reticulate. Inflorescences produced the year preceding flowering, axillary or terminal, paniculate or racemose; flowers perfect, usually fragrant, pendulous; pedicels with 1 small bract at base and 2 lateral, alternate to subopposite bracteoles near base to near apex. Calyx of 5 valvate lobes, articulated with pedicel, persistent or less commonly deciduous in fruit. Corolla urceolate to cylindrical-urceolate, sometimes strongly ridged and with conspicuous pouches between calyx lobes, with 5 short, imbricate lobes, white, usually glabrous on both adaxial and abaxial surfaces. Stamens 10 in 2 whorls, inserted at base of corolla; filaments flattened, straight or geniculate, smooth, papillose, or with long to short unicellular hairs, strongly expanded near base, with pair of stout, minutely papillose, spurlike appendages at anther-filament junction; anthers \pm ovoid, obscurely to clearly papillose, lacking apical awns, dehiscing by large, introrse-terminal, elliptic pores, usually with line of white disintegration tissue on back of each lobe but not extending into spurs; pollen tricolporate, in tetrads, without viscin strands. Stigma truncate to capitate, obscurely 5-lobed, minutely papillose; style columnar, slightly swollen near base, straight, with 5-fluted central canal, slightly to strongly impressed into apex of ovary (placentae thus appearing subapical to nearly basal with respect to apex of capsule), as long as corolla; ovary superior, 5-locular, glabrous to densely covered with unicellular hairs, the placentae axile, slightly bilobed, bearing numerous anatropous ovules; nectariferous disc an enlargement of base of ovary wall. Capsules erect, loculicidal, short-ovoid, ovoid, globose, subglobose, or slightly urceolate, with 5 unthickened sutures; placentae persistent on columella. Seeds small, brown, spindle shaped to angular-ovoid, occasionally slightly winged, end sometimes truncated, the loose, thin testa composed of single layer of elongated or \pm isodiametric (in surface view) cells; embryo small, straight, \pm allantoid, white, with 2 small cotyledons, central in cross section, nearer micropylar end to running length of seed, surrounded by fleshy endosperm.

DISTRIBUTION. A genus of seven species occurring in eastern Asia (Nepal across China and Japan to Kamchatka Peninsula and Commander Islands), eastern North America (Appalachians from Virginia and West Virginia south to northern Georgia; Coastal Plain from southern South Carolina to northern Florida and west to Mississippi), West Indies (western Cuba, Isle of Pines).

MEASUREMENTS AND TERMINOLOGY. With the exception of plant height, which was recorded in the field or taken from information included on specimen labels, all measurements included in the descriptions of specimens have been taken directly from dried herbarium material. The width of the calyx lobes was measured midway between the apex and the point where they join with adjacent lobes; the width of all other structures was measured at the widest point. All drawings of flowers, stamens, anthers, and petiole and lamina anatomy were made from material preserved in FAA, 50–70 percent alcohol, or from herbarium material previously expanded and softened by boiling in water (with a detergent solution). Drawings of capsules, seeds, and leaves were made from dried material.

Throughout the species descriptions, "pubescent" is used to refer to unicellular hairs; the distribution of multicellular hairs is described separately.

SPECIMENS EXAMINED

In the citation of herbarium specimens, abbreviations of institutions follow the sixth edition of *Index Herbariorum* (Holmgren & Keuken, 1974). Ordinarily from one to five specimens per state have been cited for species in the United States, and one specimen per major geographic locality for species of Cuba and eastern Asia. Specimens cited are arranged geographically by country and, within the larger countries, by state or province, as follows: United States (Virginia, West Virginia, Tennessee, North Carolina, Georgia, Florida, Alabama, Mississippi), Cuba (Pinar del Río, Isla de Pinos), Japan (Hokkaido, northern Honshu, central Honshu, western Honshu, Shikoku, Kyushu, Ryukyu Islands), Taiwan, Hong Kong, China (Anhwei, Chekiang, Fukien, Kwangtung, Hupeh, Kweichow, Kwangsi, Szechwan, Yunnan, Tibet), Vietnam, Burma, India (Manipur, Nagaland, Sikkim, West Bengal), Bhutan, and Nepal.

KEY TO THE SUBGENERA, SECTIONS, AND SPECIES OF PIERIS

1. Leaves entire, ca. 0.3–1.1 cm long, in whorls of 3; inflorescence a raceme with flowers similarly whorled; filaments roughened-papillose; erect to prostrate shrubs to ca. 10 cm high (subg. ARCTERICA). 7. *P. nana*.
1. Leaves with at least few teeth near apex, ca. (1)–2–13(–18) cm long, alternate or pseudoverticillate; inflorescence a raceme or panicle with spirally arranged flowers; filaments glabrous or pubescent; erect shrubs, small trees, or lianas, much taller than above (subg. PIERIS).
2. Capsule with placentae appearing central to nearly basal with respect to its apex, style thus strongly sunken into apex of ovary; seeds with \pm isodiametric testa cells (sect. PHILLYREOIDES).
3. Filaments glabrous, strongly geniculate; capsule glabrous; corolla 6–8(–8.5) mm long; habit shrublike to scandent (climbing beneath fibrous bark of *Taxodium* and at intervals producing leafy stems). . . . 4. *P. phillyreifolia*.
3. Filaments covered with short to long unicellular hairs, \pm straight; capsule densely pubescent to glabrous; corolla 8–13 mm long; habit shrubby, never scandent.
4. Capsule glabrous to very sparsely pubescent, 4–7 mm long; leaves \pm alternate, with only few serrations near apex, (0 or) 1 to 3 teeth per 2 cm at 1 cm below leaf apex; inflorescence an axillary raceme; vascular tissue of leaf midrib bifacial. 5. *P. cubensis*.
4. Capsule moderately to densely pubescent, 3.5–4.5 mm long; leaves

- pseudoverticillate, clearly toothed in distal half, proximal half \pm entire to obscurely toothed, 6 to 15 teeth per 2 cm at 1 cm below leaf apex; inflorescence a terminal or axillary panicle or raceme; vascular tissue of leaf midrib unifacial. 6. *P. swinhoei*.
2. Capsule with placentae appearing \pm subapical with respect to its apex, style thus only slightly sunken into apex of ovary; seeds with clearly elongated testa cells (sect. *PIERIS*).
5. Stems covered with stiff, multicellular, long-celled hairs in addition to smaller, biseriate-stalked, glandular-headed ones; leaves serrulate from base to apex, each tooth associated with a long-celled hair; leaves scattered; corolla markedly urceolate, strongly 5-ridged, with conspicuous pouches between calyx lobes. 3. *P. floribunda*.
5. Stems lacking stiff, multicellular, long-celled hairs, but with biseriate-stalked, glandular-headed ones; leaves nearly entire to clearly or obscurely toothed from base to apex, each tooth associated with a biseriate-stalked, glandular-headed hair (at least when young); leaves \pm pseudoverticillate; corolla cylindrical-urceolate to urceolate, neither ridges nor pouches as prominent as above.
6. Leaf with proximal 1-10(-14)% of margin entire, nearly always clearly toothed from base to apex, ca. 4.6 to 13 teeth per cm (total teeth along margin of one side of leaf divided by lamina length); 3^o veins usually forming prominent, clearly visible, often fine reticulum with 2^o veins. 2. *P. formosa*.
6. Leaf with proximal (12-)16-85(-90)% of margin entire, essentially entire except for few apical teeth to clearly toothed except near base, ca. 0.3 to 6 teeth per cm; 3^o veins less pronounced, forming \pm obscure and/or lax reticulum with 2^o veins. 1. *P. japonica*.

Pieris D. Don Subgenus *Pieris*

Erect shrubs, trees, or woody vines reaching at least 0.5 m in height at maturity. Twigs usually with heterogeneous pith. Leaves alternate or pseudoverticillate, (1-)2-13(-15) cm long; margin with at least few teeth near apex and often clearly serrulate or serrate. Flowers spirally arranged in axillary or terminal racemes or panicles. Calyx lobes persistent in fruit, usually with stomata on adaxial surface; corolla 4-13 mm long; filaments 2-7.5 mm long, glabrous or covered with short to long unicellular hairs, especially near base; anthers with clearly developed line of white disintegration tissue on back. Capsule with placentae appearing central to nearly basal with respect to its apex. Testa cells strongly elongated or isodiametric (in surface view).

DISTRIBUTION. Eastern Asia (from Nepal across China to Japan), eastern North America (Appalachians from West Virginia and Virginia to northern Georgia; Coastal Plain from South Carolina to Florida and west to Mississippi), western Cuba and Isle of Pines.

NUMBER OF SPECIES: 6.

Pieris D. Don Section *Pieris*

- Portuna* Nutt. Trans. Am. Philos. Soc. n.s. 8: 268. 1842. *Andromeda* L. sect. *Portuna* (Nutt.) Gray, Man. Bot. No. U. S. ed. 2. 253. 1856. *Lyonia* Nutt. subg. *Portuna* (Nutt.) K. Koch, Dendrol. 2: 115. 1872. *Pieris* D. Don sect. *Portuna* (Nutt.) Bentham & Hooker, Gen. Pl. 2: 588. 1876. *Andromeda* L. subg. *Portuna*

(Nutt.) Gray, Synopt. Fl. N. Am. **2**: 31. 1878. TYPE SPECIES: *Pieris floribunda* (Pursh) Benth. & Hooker.

Andromeda L. sect. *Pieris* (D. Don) Gray, Man. Bot. No. U. S. ed. 2. 254. 1856.

Lyonia Nutt. sect. *Pieris* (D. Don) K. Koch, Dendrol. **2**: 116. 1872. *Andromeda* L. subg. *Pieris* (D. Don) Gray, Synopt. Fl. N. Am. **2**: 32. 1878. TYPE SPECIES: *Pieris formosa* (Wallich) D. Don.

Venation of lamina brochidodromous to reticulodromous. Inflorescences terminal or axillary panicles or axillary racemes. Capsule with placentae appearing subapical with respect to its apex. Seeds with strongly elongated testa cells.

DISTRIBUTION. Eastern Asia (Nepal across China to Japan), eastern North America (Appalachian Mountains from West Virginia and Virginia south to northern Georgia).

NUMBER OF SPECIES: 3.

1. *Pieris japonica* (Thunb.) D. Don ex G. Don, Gen. Syst. **3**: 832. 1834.

Andromeda japonica Thunb. Fl. Jap. 181. t. 22. 1784. TYPE: Japan, "juxta Nagasaki," Thunberg (probably at UPS, not seen).

Pieris japonica (Thunb.) D. Don ex G. Don f. *pygmaea* Maxim. ex Yatabe, Ic. Fl. Jap. **2**: 107. t. 30, fig. B. 1892. *Pieris japonica* (Thunb.) D. Don ex G. Don var. *pygmaea* (Maxim. ex Yatabe) Rehder in Bailey, Cycl. Am. Hort. **3**: 1336. 1901. TYPE: from material in cultivation in Japan (not seen).

Pieris japonica (Thunb.) D. Don ex G. Don var. *albo-marginata* Rehder in Bailey, Cycl. Am. Hort. **3**: 1336. 1901. *Andromeda japonica* Thunb. var. *albo-marginata* (Rehder) Schneider, Illus. Handb. Laubh. **2**: 528. 1911. TYPE: from material in cultivation in Japan (not seen).

Pieris popowii Palibin, Bull. Herb. Boissier II. **6**: 20. 1906. *Lyonia popowii* (Palibin) Chun, Sunyatsenia **4**: 253. 1940. TYPE: China, Fukien prov., near Foochow, 1884, *Popoff* s.n. (holotype, LE?, not seen) (probably *P. japonica*, although Chun (1940) said that it is very close to *P. formosa*; exact placement of this name will await examination of type).

Pieris taiwanensis Hayata, Jour. Coll. Sci. Tokyo **30**: 169. 1911. *Pieris japonica* (Thunb.) D. Don ex G. Don subsp. *taiwanensis* (Hayata) Hatusima, Jour. Geobot. **17**: 76. 1969. *Pieris japonica* (Thunb.) D. Don ex G. Don var. *taiwanensis* (Hayata) Kitamura, Acta Phytotax. Geobot. **25**: 36. 1972. TYPE: Taiwan, Taito, Daironsan, 28 Nov. 1906, T. Kawakami & U. Moru 2184 (holotype, TAI?, not seen; photos, A!, NY!).

Pieris japonica (Thunb.) D. Don ex G. Don var. *variegata* Bean, Trees Shrubs Brit. Is. **2**: 168. 1914. *Pieris japonica* (Thunb.) D. Don ex G. Don f. *variegata* (Bean) Rehder, Bibliogr. Cult. Trees Shrubs, 530. 1949. TYPE: from material in cultivation in England (not seen).

Pieris polita W. W. Sm. & Jeffrey, Notes Royal Bot. Gard. Edinburgh **19**: 117. 1916. *Lyonia polita* (W. W. Sm. & Jeffrey) Chun, Sunyatsenia **4**: 253. 1940. TYPE: China, northwestern Fukien prov., 1914, J. de la Touche 68 (holotype, E!; isotype, K!).

Pieris koidzumiana Ohwi, Bot. Mag. Tokyo **44**: 571. 1930. *Pieris japonica* (Thunb.) D. Don ex G. Don var. *koidzumiana* (Ohwi) Masamune, Sci. Rep. Kanazawa Univ. **3**: 301. 1955. *Pieris japonica* (Thunb.) D. Don ex G. Don subsp. *koidzumiana* (Ohwi) Hatusima, Jour. Geobot. **17**: 76. 1969. TYPE: Ryukyu Islands, Utchina, 1927, S. Sonohara s.n. (holotype, KYO, not seen).

Pieris japonica (Thunb.) D. Don ex G. Don f. *crispa* Rehder, Jour. Arnold Arb. 27: 173. 1946. TYPE: cultivated in garden of Carl S. English, Jr., Seattle, Washington, U. S. A., 31 December 1945, A. Rehder s.n. (holotype, AAH!).

Shrub to small tree to ca. 4(–10) m tall, with gray to brown, longitudinally furrowed bark. Twigs terete to slightly angled, with few glandular-headed hairs, otherwise glabrous to moderately pubescent. Buds ovoid to hemispheric, essentially glabrous or with fringe of unicellular hairs along scale margins. Scales 3 to 8, imbricate, apex acute to rounded. Expanded leaves pseudovericillate; petiole 1.5–10 mm long, vascular bundle unifacial; blade widely to narrowly obovate to occasionally elliptic, (1.5–)2.5–10(–12) by 0.8–3 cm, coriaceous, the epidermis not lignified to slightly so, the apex acute to obtuse or acuminate, the base attenuate to narrowly cuneate, the margin plane to slightly revolute (especially toward base), entire except for few apical teeth to clearly toothed except near base, (i.e., proximal (12–)16–85(–90)% of leaf entire), the venation brochidodromous, 3° veins less pronounced than in *P. formosa* and forming ± obscure and/or lax reticulum with 2° veins, the adaxial and abaxial surfaces with very sparse glandular-headed hairs, often glabrescent, extremely sparsely to moderately pubescent on adaxial surface of midvein. Inflorescences axillary panicles or racemes, varying greatly in size and arising from 1 or more buds clustered at apex of branches, or occasionally terminal panicles, erect to pendulous. Pedicels 2–8 mm long, with few glandular-headed hairs, otherwise densely to sparsely pubescent; bracteoles from lower (25–)30 to upper (15–)25% of pedicel, linear to narrowly triangular, 0.5–2.5 mm long; bracts 1.5–6 mm long and similar to bracteoles, occasionally those of main inflorescence axis approaching leaves in shape and size. Calyx lobes triangular, acute at apex, 2–4.5 by 0.8–2 mm; adaxial surface very sparsely (near apex) to moderately pubescent; abaxial surface with few glandular-headed hairs, otherwise glabrous. Corolla urceolate to cylindrical-urceolate, weakly 5-ridged, 5–8 by 3–4.5(–5.5) mm, white to occasionally pink tinged. Filaments 2.5–4.5 mm long, straight, covered with long, unicellular hairs, especially near base. Style slightly impressed into apex of ovary. Capsule subglobose to short-ovoid, (2.5–)3–5 by (3.7–)4–7 mm, glabrous; placenta appearing subapical with respect to capsule apex. Seeds spindle shaped, 2–3 mm long, with testa composed of very elongated cells. $2n = 24$ (Callan, 1941). (FIGURE 3. For drawings based upon Japanese material, see Thunberg, 1784; Bailey, 1901; Yatabe, 1906; Bean, 1914; Graves, 1956; and Makino, 1961. For drawings based on Taiwanese material, see Hayata, 1912; Stapf, 1923; Kanehira, 1936; Liu, 1962; Li, 1963; and Anonymous, 1974. See Anonymous, 1974, for a drawing based on Chinese material.)

DISTRIBUTION AND ECOLOGY. Japan (chiefly western and southern Honshu, Kyushu, Shikoku), Ryukyu Islands (Okinawa), Taiwan, eastern China (Anhui, Chekiang, Fukien), near sea level to ca. 3300 m alt. (MAP 1; Horikawa, 1975.)

In Japan, near sea level to ca. 2100 m; common component of diverse temperate to warm-temperate areas (e.g., forests of *Chamaecyparis*

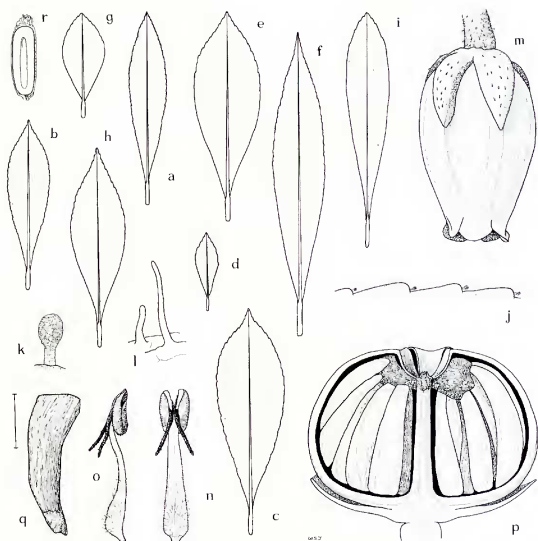
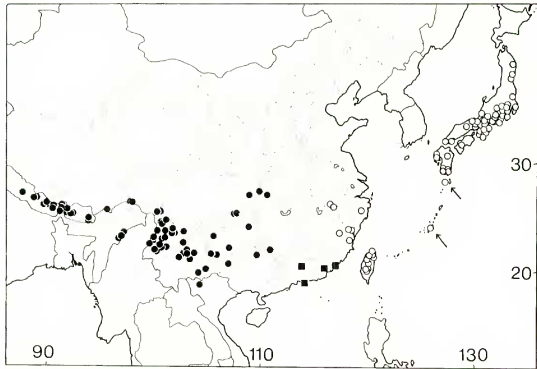


FIGURE 3. *Pieris japonica*: a-i, leaves, $\times .66$ (a-d from Japan, e-g from Taiwan, h from China, i from Okinawa); j, portion of leaf margin, $\times 8$, showing association of each serration with a multicellular, glandular-headed hair from leaf surface; k, detail of glandular-headed hair, ca. 0.1 mm long; l, unicellular hair, ca. 0.05 mm long; m, flower, $\times 4$; n, o, stamens, $\times 8.5$; p, capsule, longitudinal section, $\times 8.5$; q, seed, bar = 1 mm; r, cross section of seed, $\times 8$, showing embryo and endosperm.

obtusata, *Tsuga sieboldii*, *Abies firma*-*Illicium religiosum*, *Tsuga sieboldii*-*Rhododendron tashiroi*, *Castanopsis cuspidata*, *Cryptomeria japonica*-*Trochodendron aralioides*-*Symplocos myrtilifera*, or *Fagus crenata*). For more detailed discussion of these forest types and lists of associated species, see Tatewaki and Tsujii (1956), Tatewaki (1957), Yatoh (1960), Numata (1974). In Taiwan, in forested or open grassy areas on mountain slopes, ca. 300-3300 m alt. In eastern China, ca. 200-1500 m. In Japan and China flowering chiefly March to May; in Taiwan mainly January to March.

COMMON NAMES. Asebi (Japan, Taiwan, Ryukyu Islands), ma tsui mu shu (China; Steward, 1958), ma-tsui-mu (China; Anonymous, 1974), lily-of-the-valley bush (U. S. A.).



MAP 1. Distribution of *Pieris formosa* (dots), *P. japonica* (circles), and *P. swinhoei* (squares).

REPRESENTATIVE SPECIMENS. **Japan.** NORTHERN HONSHU: Iwate pref., Miyamori, *Muroi* 4005 (A); Miyagi pref., Hanaizumi, *Muroi* 4741 (A). CENTRAL HONSHU: Aichi pref., Ooyama, Atsumi-cho, Atsumi peninsula, *Kanai & Koyama* 742686 (TNS); Chiba pref., Mt. Kiyosumi, *Ikegami* 4753 (A); Fukui pref., Kaminaka-machi, *Makino Herb.* 59424 (MAK); Gifu pref., *Shiota* 2494 (A); Gumma pref., Momoi, *Elliott* 94 (A); Hyogo pref., Kobe, *Faurie* 5424 (w), Yamamoto, *Togasi T.S.M.* 1039 (A, E); Kanagawa pref., Mt. Kamiyama, Hakone Mts., *Mizushima* 16350 (E); Kyoto pref., SE of Kyoto-city, *Konta* 5520 (E, K, UC); Mie pref., Takihara, Oh-miya-cho, Doai-gun, *Kanai* 731114 (A, E, TAI, UC), Fudo-daki, *Okuyama* 13588 (TNS); Nagano pref., Nojiri, *Jack s.n.*, 6 Sept. 1905 (A, GH), Hiraoka-mura, *Takei T.N.S.* 148066 (TNS); Nara pref., Nara-city, *Muroi* 825 (A); Osaka pref., Tsibasi, *Muroi* 6676 (A); Saitama pref., Mt. Bukosan, *Makino Herb.* 81566 (MAK); Shiga pref., Kiyota, Kamogun, *Hashimoto T.S.M.* 847 (E, GH, NY, UC, w); Shizuoka pref., Fujinomiya, Mt. Fuji, *Hiroe* 12670 (UC); Mt. Higane, *Mizushima* 887 (A); Tokyo pref., Mt. Takamizu, *Suzuki* 10 (A); Wakayama pref., Mt. Odaigahara, *Hayakawa's Coll.* N1722 (UC), Futakawa, Nishimuro, *Ikegami* 1962 (A). WESTERN HONSHU: Okayama pref., Niizato village, Shingotown, *Hiroe* 3665 (UC); Yamaguchi pref., Yoshiki-gun, Ohuchi-mura, *Nikai* 426 (TNS). SHIKOKU: Kochi pref., Sasagamine, Tosa-gun, *Makino Herb.* 81508 (MAK). KYUSHU: Hiuga pref., Mt. Sobosan, *Faurie* 3447 (UC); Kagoshima pref., Noze, Sasutama-gun, *Muroi* 3881 (A), Takushima, *Wilson* 6002 (A, US); Nagasaki pref., Nagasaki, *Oldham s.n.*, 1862 (F, GOET, M, NY, w). RYUKYU ISLANDS: Okinawa pref., Kunigami-gun, *Sonohara* 41 (E, GH, K, L, NY, US); Kungami-mura, Awa, Tanagagumui, *Amano* 7475 (NY, TAI, TNS). **Taiwan:** I-lan Hsien, Mt. Taiping, *Chuang & Kao* 2150 (NA, UC); Taipei Hsien, Tang-ming-shan, *Chuang & Lin* 4796 (A, UC); Hokuto, *Faurie* 169 (P); Hsinchu Hsien, Yen-yang Lake, *Huang* 5489 (TAI); Chiayi Hsien, Pai-ying hostel to Tung-pu, *Kueh* 1352 (TAI); Kagi prov., Arisan, *Wilson* 9777 (A, US). **China.** ANHWEI: Chimen, *Ching* 3134 (A, E, UC); Wu Yuen, *Ling* 7850 (UC).

CHEKIANG: Yun Fun, near Taichow, *Ching* 1324 (A, E, NA, P, UC). FUKIEN: Kuliang, Foochow, *Carles* 667 (E); Kuliang, *Chung* 6700 (A); Shouning, *Ching* 2254 (A, E, K, UC, US); Yenping, *Dunn* 2894 (A).

Pieris japonica is a rather variable and widely distributed species occurring in Japan, the Ryukyu Islands, Taiwan, and China. The populations occurring in each of these four areas have been considered by many botanists to be distinct species (*P. japonica*, *P. koidzumiana*, *P. taiwanensis*, and *P. polita*, respectively). However, after a careful study of this group across its entire range, it was found that the characters that supposedly distinguish these taxa are inconsistent and/or intergrade extensively (see FIGURE 4), and it is often impossible to determine from morphological criteria whether a particular individual was collected in Japan, Taiwan, the Ryukyu Islands, or China. Therefore, these taxa are considered to be conspecific. The major morphological differences between these geographically disjunct populations of *P. japonica* are indicated in FIGURE 4.

Individuals from Japan (group B) usually have obovate leaves with the proximal 15–45(–60) percent of the margin entire and from ca. 2.5 to 6 teeth/cm, and flowers in pendent to (less commonly) more or less horizontal or erect panicles or racemes. The Chinese plants (group C) are very similar to those of Japan except that they have slightly less strongly toothed leaves (i.e., proximal 30–70% of leaf margin entire and from ca. 1.5 to 4 teeth/cm). These plants were described as a species distinct from *P. japonica* because of their supposed exclusively racemose inflorescence (see Smith, 1916). However, paniculate inflorescences are common, especially in plants that appear to be growing vigorously (see *Ching* 1324 (A, UC), *Ching* 2527 (K, UC), *Chung* 6510 (A), *Chung* 6700 (A), *Ling* 7850 (UC)), and both panicles and racemes can be found on the same plant. Because of the lack of any characters unambiguously separating these populations from those of Japan, they are here considered to be conspecific. Steward (1958) also thought that these Chinese populations were *P. japonica*.

The Taiwanese plants (group D) are also very similar to those of Japan; however, they not only tend to have leaves with fewer teeth (i.e., proximal 30–70% of leaf margin entire, and ca. 1.5 to 4 teeth/cm) but also frequently have more coriaceous leaves, and flowers in often robust, erect to (less commonly) more or less horizontal or drooping panicles or racemes. The plants of Taiwan have traditionally been recognized as a distinct species on the basis of their erect paniculate inflorescences (see Hatusima, 1969). However, this character can not be consistently used because occasional Japanese plants (e.g., *Faurie* 5424 (w); *Makino s.n.*, 30 March 1938 (L); *Miyamoto s.n.*, 9 April 1970 (A); *Bisset* 4505 (E)) have erect panicles, and plants with more or less horizontal inflorescences (e.g., *Chuang & Lin* 4796 (A, UC)) do occur in Taiwan. Stapf (1923) has noted that "the variation [within *P. taiwanensis*] from erect racemes to such as droop after the fashion of *P. japonica* is remarkable," and he stated that "it appears to be quite independent of external conditions, both extremes occurring in the same sowing." Stapf also correctly pointed out that Japanese collections usually have "smaller thinner leaves, more finely crenulate from the base, slenderer raceme-spindles and

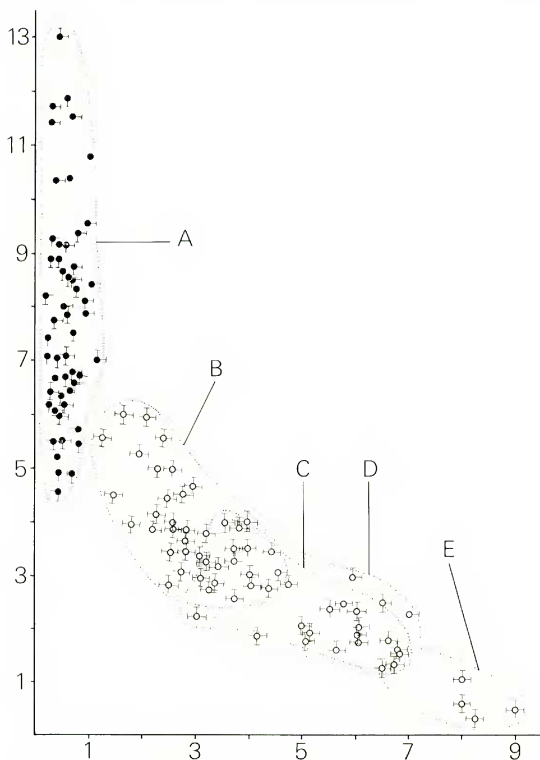


FIGURE 4. Scatter diagram showing variation in 7 characters within *Pieris japonica* and *P. formosa*. Vertical axis = number of teeth/cm (averaged across total lamina length), horizontal axis = % of leaf margin entire; solid circles = 3° leaf veins forming ± prominent, clearly visible, often fine reticulum with 2° veins, open circles = 3° veins less pronounced, forming ± obscure and/or lax reticulum with 2° veins; full tail up = angle of leaf base < 50°, no tail up = angle of leaf base ≥ 50°; full tail to right = leaves obovate, no tail to right = leaves elliptic, half tail to right = ± intermediate; full tail down = panicles with 3 or more lateral branches, half tail down

pedicels and smaller flowers'' than do Taiwanese populations. However, the above-mentioned characters fail consistently to separate plants of the two geographic areas since some Taiwan specimens have slender inflorescence axes, small flowers, and only moderately coriaceous leaves and are thus identical to some Japanese or Chinese collections. The populations of Taiwan and Japan (as well as China) are thus considered to be conspecific, in agreement with the opinions of Kitamura and Murata (1972) and Hatusima (1969).

Finally, the plants of the Ryukyu Islands (group E) are quite similar to those of Japan or China, differing only in their usually slightly more coriaceous and typically narrowly obovate leaves with only (1 or) 2 to 4 (to 11) teeth near the apex (i.e., proximal 67-90% of the leaf margin entire and ca. 0.3 to 1.5 teeth/cm). The plants produce pendent to more or less horizontal panicles or racemes. These small populations found only on the island of Okinawa are more easily distinguished than those of China, Japan, or Taiwan. However, they are included here within a broadly defined *P. japonica* since there is no clear morphological gap in either leaf shape or marginal dentation between the Ryukyu plants and those of China or Taiwan. A similar conclusion was reached by Hatusima (1969) and Walker (1976).

Pieris japonica, as here defined (FIGURE 4, groups B-E), is very closely related to *P. formosa* (group A), from which it can consistently be distinguished by its more sparsely toothed leaves (i.e., proximal (12-)16-85(-90)% of leaf margin entire with ca. 0.3 to 6 teeth/cm vs. proximal 1-10(-14)% of leaf margin entire with ca. 4.6 to 13 teeth/cm in *P. formosa*). The leaves also have less pronounced tertiary veins that form an obscure and/or lax reticulum with the secondary veins vs. leaves with tertiary veins forming a prominent, clearly visible, and often fine reticulum. In addition, *P. japonica* tends to have attenuate- to cuneate-based leaves more frequently. Kitamura and Murata (1972) considered *P. formosa* to be only a subspecies of *P. japonica*, but since these two taxa can be easily separated by several criteria (see FIGURE 4), and since no intermediate plants have been found, they have been maintained here as separate species. The two species are of course reproductively isolated since they are completely allopatric, although fertile hybrids (e.g., *Pieris* 'Forest Flame'; see Meyer 10733, NA) are known in cultivation.

Plants of *Pieris japonica* were introduced early into cultivation and are beautiful and popular ornamental shrubs in many temperate regions; several cultivars have been developed (see Bailey, 1901; Yatabe, 1906; Rehder, 1940; Wagenknecht, 1961; Brown, 1973; Bailey *et al.*, 1976; and Bean, 1976).

= panicles with 1 or 2 lateral branches, no tail down = racemes; full tail to left = pendent inflorescences, no tail to left = erect inflorescences, half tail to left = \pm intermediate. Group A, specimens of *P. formosa*; groups B-E, specimens of *P. japonica*: B, Japanese populations; C, Chinese populations; D, Taiwanese populations; E, Ryukyu Is. populations.

This species contains a physiologically active and toxic substance of unknown composition that has been called andromedotoxin; this compound has been known to cause livestock poisoning (Yatabe, 1906; Kingsbury, 1964).

2. **Pieris formosa** (Wallich) D. Don, *Edinburgh New Philos. Jour.* **17**: 159. 1834.

Andromeda formosa Wallich, *Asiatic Res.* **13**: 395. 1820. *Lyonia formosa* (Wallich) Hand.-Mazz. *Symb. Sinicae* **7**: 790. 1936. *Pieris japonica* (Thunb.) D. Don ex G. Don subsp. *formosa* (Wallich) Kitamura, *Acta Phytotax. Geobot.* **25**: 37. 1972. TYPE: Nepal, no definite locality, 1818, *N. Wallich* (holotype, not seen; presumed isotypes, A!, K(2 sheets)!).

Pieris bodinieri Lévl. *Bull. Acad. Géogr. Bot.* **12**: 253. 1903. TYPE: China, Yunnan, "environs de Yun-nan-sen, c, dans la montagne," 9 March 1897, *Fr. Ducleux* 60 (lectotype, w!).

Pieris forrestii Harrow, *Notes Royal Bot. Gard. Edinburgh* **8**: 196. 1914. *Pieris formosa* (Wallich) D. Don var. *forrestii* (Harrow) Airy Shaw, *Curtis's Bot. Mag.* **157**: t. 9371. 1934. TYPE: China, Yunnan; Harrow's description based on plants growing in nurseries of Bees Limited and in Royal Botanic Garden, Edinburgh, from seed collected by George Forrest. Not seen.

Pieris huiana Fang, *Contr. Biol. Lab. Sci. Soc. China Bot.* **10**: 240. 1938. TYPE: China, Yunnan, near Yunnansen [Kun-ming-Hsien], *E. E. Maire* 1361 (lectotype, E!; fragments of lectotype, A!).

Pieris formosa (Wallich) D. Don f. *longiracemosa* Fang, *Contr. Biol. Lab. Sci. Soc. China Bot.* **10**: 240. 1938. TYPE: China, Yunnan, Lu-feng-hsien, 1700 m alt., 26 June 1933, *H. T. Tsai* 53567 (holotype, PE?, not seen; isotype, A!).

Shrub to small tree to 5(–10) m tall, with gray to brownish, longitudinally furrowed bark. Twigs terete to slightly angled, with few glandular-headed hairs, otherwise glabrous to densely pubescent. Buds ovoid to hemispheric, glabrous or with fringe of unicellular hairs along scale margins. Scales 3 to 8, imbricate, apex acute to rounded. Expanded leaves pseudoverrucillate; petiole 2–16 mm long, vascular bundle unifacial; blade widely to narrowly elliptic or obovate, (2–)2.5–10(–18) by 0.8–3.5(–5.5) cm, coriaceous, the epidermis lignified, the apex acute or obtuse to acuminate or mucronate, the base narrowly cuneate to rounded, the margin plane to slightly revolute (especially toward base), nearly always clearly toothed from base to apex (i.e., proximal 1–10(–14)% of leaf entire); the venation brochidodromous to reticulodromous, 3° veins usually forming prominent, clearly visible, often fine reticulum with 2° veins, the adaxial and abaxial surfaces with very sparse glandular-headed hairs, glabrescent, sparsely to densely pubescent on adaxial surface of midvein. Inflorescences axillary panicles or racemes, varying greatly in size and arising from 1 or more of buds clustered at apex of branches, or occasionally terminal panicles, erect to pendulous. Pedicels 2–9 mm long, with few glandular-headed hairs, otherwise usually densely pubescent; bracteoles from lower (10–)15 to upper (25–)30% of pedicel, linear to narrowly triangular or ovate, 0.8–1.8 mm long; bracts 2–5.5 mm long, ovate to obovate, occasionally those of main inflorescence axis approaching leaves in shape and size. Calyx lobes triangular, acute at apex, 2–4.5 by 1–2 mm; adaxial surface very sparsely (near apex) to densely pubescent; abaxial

surface with few glandular-headed hairs, otherwise glabrous or very sparsely pubescent near base. Corolla urceolate to cylindrical-urceolate, weakly 5-ridged, 4-9(-12) by 3.5-5.5(-8) mm, white to occasionally pink tinged. Filaments 2-4.5 mm long, straight, covered with long, unicellular hairs, especially near base. Style slightly impressed into apex of ovary. Capsule ovoid to short-ovoid, globose, or subglobose, 3-6 by (3.5-)4-7 mm, glabrous; placenta appearing subapical with respect to capsule apex. Seeds spindle shaped, 2-3 mm long, with testa composed of very elongated cells. $2n = 24$ (Wood, 1961; Mehra & Bawa, 1969). (FIGURE 5; see also Wight, 1850; Skan, 1909; Airy Shaw, 1934; Anonymous, 1974.)

DISTRIBUTION AND ECOLOGY. Southwestern China (Hupeh, Kweichow, Kwangsi, west to Szechwan, Yunnan), Vietnam, along Himalayas to Nepal. (MAP 1.) Various broadleaved forests (e.g., *Symplocos pyrifolia*, *Quercus semecarpifolia*, or *Rhododendron arboreum*), *Tsuga dumosa* or *Pinus* forests, grassy and/or rocky ridges, thickets, open slopes, and ravines, or along streams, (500-)1700-3300(-3800) m alt. For more information on some of these forest types and lists of associated species, see Wang (1939) for Yunnan, Kingdon-Ward (1941), 1945) for Burma, Stainton (1972) and Ohashi (1975) for Nepal. Flowering chiefly late February to early June, varying greatly with altitude and latitude.

COMMON NAMES. Bolú (Nepal; *Lace* 2270 (E)); sheabogee, chemala (Nepal; Wallich, 1820); mei-li ma-tsui-mu (China; Anonymous, 1974).

REPRESENTATIVE SPECIMENS. **China.** HUPEH: Patung Hsien, *Chow* 1028 (A, E, NY); Hsin Tien-tsze, *Chun* 4045 (A). KWEICHOW: Pin-fa, *Cavalerie* 9 (A, E); Yinkiang, *Tsiang* 7594 (E, NY, UC); Pichieh, *Tsiang* 8991 (E, NY, UC, W); Anlung, *Tsiang* 9369 (A, E, US); Feng Ching Shan, Ma-chao Ho, *Steward et al.* 759 (A). KWANGSI: Tzu-yuan Hsien, *Chung* 83526 (A); Ling Yun Hsien, Lao Shan, *Steward & Cheo* 71 (A, E, W); San Chiang Hsien, Ling Wang Shan, *Steward & Cheo* 983 (A, NY, W). SZECHWAN: Nan-chuan Hsien, Chin-fo Shan, *Fang* 597 (A); Yalung, Yen-yuen, 28°10' N, *Handel-Mazzetti* 2612 (W); Mou-tao-chi, vic. of Wan-hsien, *Hwa* 44 (A); Wushan, *Wilson* 442 (K, NY). YUNNAN: Tung-kwei valley, *Bulley* 446 (A); Tze-li, on Yangtze, *Ching* 20259 (A); Ganhai-tze, SW Likiang Snow Range, *Ching* 21724 (A); Wen-feng-tze, SW end of Likiang valley, *Ching* 21818 (A); N of Kunming, *Feng* 80 (A); Chien-chuan, *Feng* 241 (A); Yung-ping Hsien, *Forrest* 5027 (A, E); E flank of Likiang Range, 27°15' N, *Forrest* 5875 (E); W flank of Shweli-Salween Divide, 25°20' N, *Forrest* 8945 (A, E); Salwin-Kui-chang Divide, 27° N, 98°35' E, *Forrest* 25763 (E, K); Mengtse, *Henry* 11295 (A, E, NY); Yunnan-sen, *Maire* 1063 (UC); Ta-li, San Yong Mt., *McLaren's Coll.* C40 (A, E); Lake of Tali-fu, Tsangshan Range, between Tatzang and Hsia-Kuan, *Rock* 3100 (A, E, UC, US, W); Tali plain, Lake of Talifu, Tsangshan, *Rock* 3171 (A); between Talifu and Likiang to foot of Likiang Snow Range, *Rock* 3264 (A, US); Shweli-Salween Divide, E of Tengyueh, *Rock* 7647 (A, UC); between Tengyueh and Likiang-fu, *Rock* 8075 (A, UC); Chiu-pei Hsien, *Tsai* 51439 (A, E); Tung-jen Hsien, *Tsai* 52827 (A); Shang-pa Hsien, *Tsai* 56597 (A, E); Wei-se Hsien, *Tsai* 57878 (A, E); Cheng-kiang, Tung-lung-tang, *Tsang & Wang* 16320 (A); Li-kiang Hsien, *Wang* 70472 (A, TAI); Chungtien, Haba, *Yü* 14986 (A, E); Lichiang, Snow Range, *Yü* 15045 (A, E). **TIBET:** Chumbi, *King's Coll.* 556 (E); Migytun, Tsari Chu, 28°40' N, 93°38' E, *Ludlow et al.* 6624 (E); Trulung, Po-Tsangpo valley, Pome, *Ludlow et al.* 12270 (E); Showa, Po-Tsangpo valley, *Ludlow et al.* 12508 (E). **Vietnam:** Tonkin, Massif du Phan-si-Pan, Lao Kay, *Poilane* 17127 (P). **Burma:** N'Maikha-

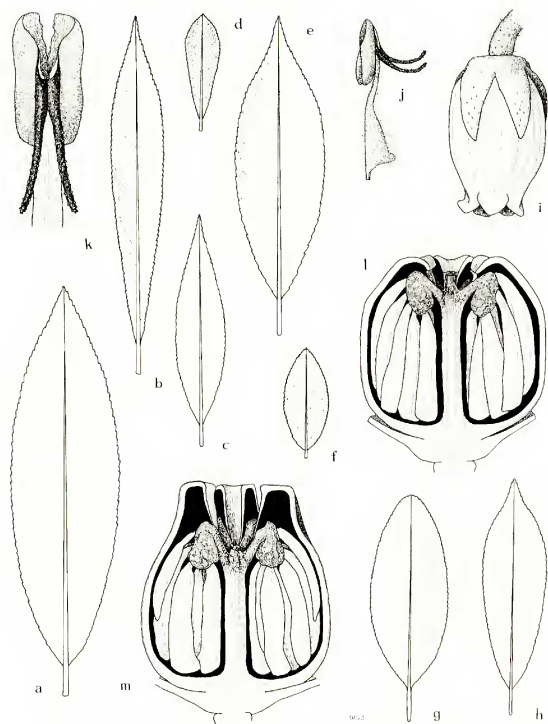


FIGURE 5. *Pieris formosa*: a-h, leaves, $\times .66$; i, flower, $\times 4$; j, stamen, $\times 8.5$; k, anther, $\times 17$; l, m, capsule, longitudinal section, $\times 8.5$.

Salwin Divide, near Tzi-san Ho, $26^{\circ}18' N$, $98^{\circ}48' E$, *Forrest 26518* (NY, P, US, W); Panwa Pass, *Kingdon-Ward 394* (A, E). **INDIA**. MANIPUR: Sirohifur, *Watt 5960* (E). NAGALAND: Naga Hills, Japoo, Kohima, $25^{\circ}40' N$, $94^{\circ}10' E$, *Kingdon-Ward 7719* (K). SIKKIM: Lachen, *Biswas 6883* (A); Zenni Valley, *Smith & Cave 2720* (B). WEST BENGAL: Darjeeling Distr., Sandakphi, *Lace 2270* (E); Singalila Range, Mt. Tonglu, *Vos & Corbett 39* (E). **BHUTAN**: Bela Djong, Paro, *Cooper 3566* (E); Ha area, *Gould*

44 (E); 20 mi S of Trashigang, *Kingdon-Ward 6426* (E); Yonpu La, *Ludlow & Sherriff 1146* (E); Chumbi valley, Arno Chu R., *Ludlow et al. 16005* (A, E). **Nepal:** Chepua to Hatia, *Banerji s.n.*, 15 May 1965 (A); Namche Bazar, *Jionor 34* (E, K); Marsiandi Valley, *Lowndes 897* (A, E); Khumbu, Namche Bazar, *Poelt s.n.*, 8 Oct. 1962 (M); Arun Valley, Maghang Khola, E of Num, *Stainton 232* (A, E); S of Dhorpatan, *Stainton et al. 335* (A, E); Rambrong, Lamjung Himal., *Stainton et al. 8297* (E).

Pieris formosa is most closely related to *P. japonica*, from which it is easily distinguished by its much more prominently serrate and often wider-based leaves (FIGURE 4; see also key). In addition, the tertiary veins are more prominent, forming a clearly visible and fine reticulum with the secondary veins. The two species are completely allopatric (MAP 1).

This species is quite variable in the development of the inflorescences and in the size of the leaves and flowers (the latter especially in Yunnan). Some plants produce only short racemes, while others produce large, many-branched panicles. In some individuals the panicle has up to 15 branches. However, intermediate conditions are extremely common, and often racemes and panicles can be found on the same plant. Some plants consistently produce small leaves only 3–4 cm in length, while others have large leaves of ca. 10–15 cm; corolla length varies from 4 to 12 mm. The presence of large leaves and flowers is strongly correlated, and individuals with such large leaves and flowers have been described as *Pieris forrestii*. The continuous range of intermediate plants that connect this form with plants bearing small leaves and flowers make untenable the recognition of this morphological form at either specific or varietal rank. Even Airy Shaw (1934), who recognized the large-leaved plants as a distinct variety, stated: "Examination of the ample Chinese, Indian and cultivated material of *P. formosa* and *P. Forrestii* in the Kew Herbarium shows that the latter constitutes what may be termed the 'grandiflora' end of a long series, between the members of which no hard and fast lines can be drawn."

Plants of this species are perhaps the most beautiful of any in the genus and are commonly cultivated in temperate areas of the northern hemisphere; however, they are not as hardy as those of *Pieris japonica*. Several cultivars have been developed (see Brown, 1973; Wagenknecht, 1961; Bean, 1976).

3. *Pieris floribunda* (Pursh) Bentham & Hooker, Gen. Pl. 2: 588. 1876.

Andromeda floribunda Pursh in Sims, Curtis's Bot. Mag. 38: t. 1566. 1813. *Leucothoë floribunda* (Pursh) D. Don, Edinburgh New Philos. Jour. 17: 159. 1834. *Zenobia floribunda* (Pursh) DC. Prodr. 7: 598. 1839. *Portuna floribunda* (Pursh) Nutt. Trans. Am. Philos. Soc. II. 8: 268. 1843. *Lyonia floribunda* (Pursh) K. Koch, Dendrol. 2: 155. 1872. TYPE: United States, "the mountains of Georgia," 1811, *J. Lyons s.n.* (not seen).

Andromeda montana Buckley, Am. Jour. Sci. Arts 45: 172. 1843. Type: "Mts. Carol," *S. B. Buckley* (lectotype (here designated), GH!; possible duplicates of lectotype, NY!, GA!).

Andromeda vacciniifolia K. Koch, Dendrol. 2: 116. 1872, *pro. syn.* (under *Lyonia floribunda*).

Shrub to ca. 2 m tall, with grayish to brownish, longitudinally furrowed bark. Twigs terete to occasionally very slightly angled, with few glandular-

headed hairs, conspicuously strigose due to presence of large, stiff, long-celled hairs, otherwise sparsely to densely pubescent. Buds ovoid, with few glandular-headed hairs, otherwise glabrous or nearly so. Scales 4 to 6, imbricate, apex long- to short-acuminate. Expanded leaves alternate; petiole 4–11 mm long, vascular bundle unifacial; blade elliptic to ovate, (1.5–)3–7.2 by (0.6–)1–2.8 cm, coriaceous, the epidermis nonlignified, the apex acute, the base rounded to widely cuneate, the margin plane, serrulate, each serrulation associated with a long-celled hair, the venation \pm reticulodromous, 3° veins clearly visible, the adaxial and abaxial surfaces with sparse glandular-headed hairs, glabrescent, sparsely to densely pubescent on adaxial surface of midvein. Inflorescences terminal panicles, sometimes with lowermost lateral branches of panicle arising from axils of uppermost foliage leaves, erect. Pedicels 2–4.5 mm long, with few glandular-headed hairs and often few long-celled hairs, otherwise densely pubescent; bracteoles from lower 25% to near middle of pedicel, linear to narrowly triangular, 0.9–2.3 mm long; bracts 2–9 mm long, similar to bracteoles in shape, often those of primary inflorescence axis approaching leaves in shape and size. Calyx lobes triangular, acute at apex, 2–4 by 1–1.7 mm; adaxial surface densely pubescent near apex; abaxial surface with few glandular-headed hairs, sometimes also with long-celled hairs, otherwise glabrous or sparsely pubescent. Corolla urceolate, strongly 5-ridged and with conspicuous pouches between calyx lobes at base, 4–7 by 3–5.5 mm, white. Filaments 2–3 mm long, straight, covered with unicellular hairs, especially near base. Style slightly impressed into apex of ovary. Capsule subglobose or globose to ovoid, 4–6 by 4–6 mm, glabrous; placentae appearing subapical with respect to capsule apex. Seeds spindle shaped, 2.5–3.5 mm long, usually \pm flattened, with 2 inconspicuous wings, with testa composed of very elongated cells. (FIGURE 6; see also Sims, 1813; Britton & Brown, 1913; Bean, 1914; Small, 1920, 1933; Gleason, 1952; Graves, 1956; Ingram, 1963; Radford, Ahles, & Bell, 1968; Strausbaugh & Cove, 1973.)

DISTRIBUTION AND ECOLOGY. Eastern United States from West Virginia and Virginia to northern Georgia, in Appalachian Mountains. (MAP 2.) Frequently on rocky ridges or slopes, in thickets, *Tsuga* forests, *Quercus* and/or *Pinus* forests, or mountain balds, ca. 500–1750 m alt. Flowering April to June.

COMMON NAMES. Mountain fetter-bush, fetter-bush.

REPRESENTATIVE SPECIMENS. **United States.** WEST VIRGINIA. Pendleton Co.: High Knob, Shenandoah Mt., *Allard 9667* (GH, US). Pocahontas Co.: 1 mi W of Arborvale, *Gray s.n.*, 3 March 1922 (A). VIRGINIA. Augusta Co.: Allegheny Mts., Reddish Knob, *Killip 36002* (NY, US, W). Amherst Co.: trail from Rocky Row Run to Blue Ridge Pkwy., NW of Slaty Gap, *Freer 2588* (GH). Bath Co.: NW slope of Beard's Mt., *Zobel s.n.*, 6 Nov. 1966 (DUKE). Craig Co.: W of Craig's Creek, 6 mi NE of New-castle, *Wherry & Adams 2683* (A, GH). Patrick Co.: Pinnacles of Dan, ca. 4.5 mi SW of Meadows of Dan, *Jones 2650* (DUKE, F, NY). Pulaski Co.: Peak Mt., *Small s.n.*, 16 July 1892 (DUKE, F, NY, US). Rockbridge Co.: Buena Vista, near Lexington, *Churchill s.n.*, 1 Sept. 1924 (GH). Roanoke Co.: ca. 4 mi N of Hanging Rock, McAffe Knob, *Wood 5887* (GH). Rockingham Co.: Shenandoah Mt., *Hunnell*

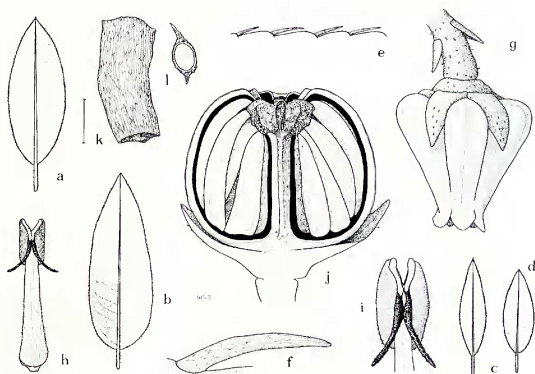
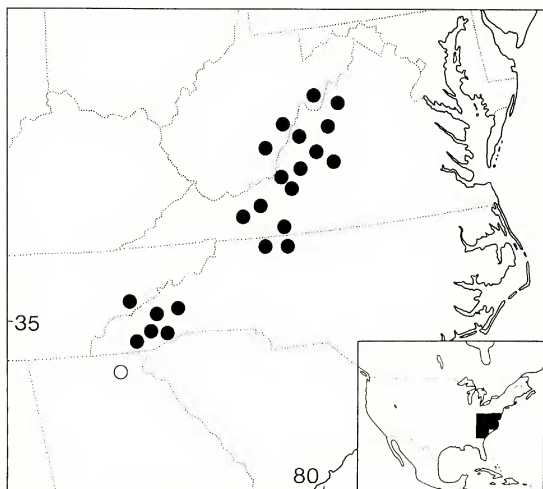


FIGURE 6. *Pieris floribunda*: a-d, leaves, $\times .66$; e, portion of leaf margin, $\times 8$, showing association of each serration with a multicellular hair; f, multicellular, long-celled hair from leaf margin, ca. 1 mm long; g, flower, $\times 4$; h, stamen, $\times 8.5$; i, anther, $\times 17$; j, capsule, longitudinal section, $\times 8.5$; k, seed, bar = 1 mm; l, cross section of seed showing "wings."

13182 (GH). TENNESSEE. Sevier Co.: on Mill Creek Trail to Mt. Le Conte, *Sharp & Underwood 740* (NY). NORTH CAROLINA. Haywood Co.: Mt. Pisgah, *Walton 3563* (DUKE). Surry Co.: Big Pinnacle, Pilot Mt., *Williams 425* (DUKE). Transylvania Co.: N of Devil's Courthouse, Blue Ridge Pkwy., *Bozeman et al. 9119* (E). Jackson Co.: Tennessee Bald, Jackson-Transylvania Co. line, *Wherry s.n.*, 17 July 1935 (A).

Pieris floribunda is a rather uniform species that is distinctive and is easily distinguished from all other members of the genus. It is most closely related to *P. formosa* and *P. japonica*, with which it shares the characters of elongated seed-coat cells and capsules with subapical placentae. However, it can readily be distinguished from these two species by its alternate leaves, its strigose stems (i.e., with stiff, multicellular, long-celled hairs in addition to multicellular, biseriate-stalked, glandular-headed ones), its serrulate leaves with each serrulation associated with a long-celled hair, and its more strongly ridged corolla with conspicuous pouches between the calyx lobes. Indeed, this species is so distinctive that Nuttall (1843) placed it in the monotypic genus *Portuna*.

Individuals of *Pieris floribunda* are beautiful, cold-hardy shrubs and are frequently cultivated, especially in the cooler areas of eastern North America. Several cultivars are available (see Wagenknecht, 1961). Because of the ornamental qualities of this species and *P. japonica*, several attempts have been made to hybridize them. All of these attempts have failed, resulting either in no seed production or in seed that failed to produce viable offspring



MAP 2. Distribution of *Pieris floribunda* (open circle = type collection, given as "the mountains of Georgia").

(Jaynes, 1975). However, an unusual seedling, which is very probably a hybrid between these two species, has been discovered in a group of seedlings grown from seed of plants of *P. floribunda* that had been growing in cultivation near plants of *P. japonica*. This individual has been reproduced by cuttings and is known as 'Brouwer's Beauty'. It is morphologically intermediate (even in the structure of its multicellular hairs) between the two supposed parental species and is sterile (Jaynes, 1975, and pers. obs.; see Mazzeo & Ayers 37135 (NA)).

Pieris D. Don Section **Phillyreoides** Bentham & Hooker,
Gen. Pl. 2: 588. 1876.

Ampelothamnus Small, Shrubs Florida, 96. 1913. TYPE SPECIES: *Pieris phillyreifolia* (W. J. Hooker) DC.

Venation of lamina brochidodromous. Inflorescences terminal or axillary racemes, rarely terminal panicles. Capsule with placentae appearing central to nearly basal with respect to its apex. Seeds with \pm isodiametric testa cells.

DISTRIBUTION. Southeastern China (Kwangtung and Fukien), southeastern U. S. Coastal Plain (South Carolina to Florida, west to Mississippi), western Cuba and Isle of Pines.

NUMBER OF SPECIES: 3.

4. **Pieris phillyreifolia** (W. J. Hooker) DC. Prodr. 7: 599. 1839.

Andromeda phillyreifolia W. J. Hooker, Ic. Pl. 2: t. 122. 1837. *Ampelothamnus phillyreifolius* (W. J. Hooker) Small, Shrubs Florida, 96. 1913. TYPE: United States, Florida, Apalachicola, *Drummond* 27 (holotype, E!; isotype, E!; possible isotype, an unnumbered specimen of *Drummond* collected at Apalachicola, GH!). *Andromeda croomia* Torrey ex A. Wood, Class-book Bot. 487. 1861. TYPE: United States, Florida, damp woods, Quincy, A. Wood s.n. (holotype, NY!).

Rhizomatous shrub to ca. 1 m tall, with brownish to gray, longitudinally furrowed bark, or more commonly lianas, climbing within fibrous bark of *Taxodium ascendens* (or *Chamaecyparis thyoides*) to ca. 10 m by means of flattened rhizomes bearing scalelike leaves that at intervals give rise to lateral branches bearing large photosynthetic leaves. Twigs \pm terete, with few glandular-headed hairs, otherwise sparsely to moderately pubescent. Buds ovoid, glabrous or with fringe of unicellular hairs along scale margins. Scales 3 to 6, imbricate, apex acute to acuminate. Expanded leaves \pm pseudovercillate; petiole 1.5–6.5 mm long, vascular bundle unifacial; blade ovate, elliptic, or slightly obovate, (1–)2–6(–7) by (0.3–)0.5–2(–2.7) cm, very coriaceous, the epidermis strongly lignified, the apex acute to rounded, the base narrowly cuneate to rounded, the margin clearly revolute (especially toward base), obscurely to clearly toothed and always with several obvious serrations near leaf apex, the venation brochidodromous, 3^o veins obscure to slightly raised and reticulate, the adaxial and abaxial surfaces with sparse glandular-headed hairs, glabrescent, sparsely pubescent on adaxial surface of midvein. Inflorescences axillary racemes from 1 or several of buds near apex of branches, \pm horizontal. Pedicels 2–7.5 mm long, with few glandular-headed hairs, otherwise usually densely pubescent; bracteoles from upper 15% to near middle of pedicel, linear to narrowly triangular, 0.7–2 mm long; bracts 1–2 mm long, similar to bracteoles in shape. Calyx lobes elongate-triangular, acute at apex, 3.5–5 by 1–1.5 mm; adaxial surface sparsely pubescent or merely papillose near apex; abaxial surface with few glandular-headed hairs. Corolla cylindrical-urceolate, weakly 5-ridged, 6–8(–8.5) by 4–5 mm, white. Filaments 4–6 mm long, geniculate, glabrous, \pm smooth. Style strongly impressed into apex of ovary. Capsule subglobose, 2.5–4 by 3.5–5.3 mm, glabrous; placentae appearing central to nearly basal with respect to capsule apex. Seeds angular-ovoid, 0.9–1.3 mm long, with testa of \pm isodiametric cells. (FIGURE 7; see also Hooker, 1837; Small, 1933; Lemon, 1945; Lemon & Voegel, 1962; Godfrey & Wooten, 1981.)

DISTRIBUTION AND ECOLOGY. Eastern United States from southeastern South Carolina to Florida, west to Mississippi. (MAP 3; see also Ingram, 1963; Duncan, 1967; Godfrey, 1969; Clark, 1971.) Coastal Plain species occurring

in *Taxodium ascendens* or *Chamaecyparis thyooides* swamps, less commonly in various broad-leaved swamps (of *Nyssa biflora*, *Acer rubrum*, *Magnolia virginiana*, *Cyrilla racemiflora*, or *Cliftonia monophylla*) or low pine-lands. Flowering chiefly late January through April.

COMMON NAMES. Climbing heath, climbing fetter-bush.

REPRESENTATIVE SPECIMENS. **United States.** SOUTH CAROLINA. Charleston Co.: 4.5 mi S of Santee R. along U. S. Rte. 17, *Godfrey 68211* (FSU). Colleton Co.: Moselle Swamp, W of Islandton, *Godfrey 68534* (FSU). GEORGIA. Atkinson Co.: S of Pearson, *Bozeman 9432* (E. FSU, GH, NO, NY). Berrien Co.: Alapaha, *Cooper s.n.*, 17 February 1946 (DUKE). Charlton Co., Okefenokee Swamp between Bugaboo Landing and Bugaboo Is., *R. M. Harper 1475* (A, E, GH, US). Early Co.: Big Cypress area, near Baker Co. line, *Thorne & Ford 1868* (NY, US). Lowndes Co.: 2 mi E of Valdosta, *R. M. Harper 2052* (A, GH, US). Screven Co.: 15 mi N of Statesboro, *Godfrey 68190* (FSU). Ware Co.: Waycross, *Williamson s.n.* (NY); Wheeler Co.: 1.2 mi NE of Lumber City, *Duncan et al. 16961* (GA). FLORIDA. Bay Co.: W of Panama City, S32, T3S, R15W, *Laessle s.n.*, 21 June 1962 (FLAS). Columbia Co.: 12 mi N of Lake City, *Arnold & West s.n.*, 29 February 1948 (FLAS). Franklin Co.: S16, T7S, R7W, *Conde s.n.*, Sept. 1976 (FLAS). Hamilton Co.: 5 mi E of Jasper, *West & Arnold s.n.*, 30 Sept. 1941 (FLAS). Jackson Co.: 6 mi W of Sneads, *Wiegand & Manning 2344* (GH). Lake Co.: Alexander Springs, *Lakela 26824* (GH). Leon Co.: 12 mi W of Tallahassee, *Godfrey 58002* (GH). Liberty Co.: S of Sumatra, *Reese 1142* (GH). Madison Co.: 5 mi E of Pinella, *Kral 6290* (FSU, GH). Marion Co.: 5 mi NE of Juniper Springs, *Ward & Will 3025* (FLAS, GH). Santa Rosa Co.: W of Milton, *Godfrey & Hauk 62560* (FLAS). Taylor Co.: 3 mi NW of Perry, *Godfrey 58046* (FSU, GH). Walton Co.: 4.5 mi W of Fort Walton, *Godfrey 68388* (FSU). ALABAMA. Geneva Co.: 6.4 mi S of Hartford, *McDaniel 7628* (FSU). Mobile Co.: pine barren streams, *Mohr s.n.*, 20 February 1894 (NY). MISSISSIPPI. Jackson Co.: Escatawpa, *Demaree 32688* (GH).

Pieris phillyreifolia is a very distinctive taxon immediately recognizable because of its often scandent habit and its strongly geniculate, glabrous filaments. It is probably most closely related to *P. cubensis*, which, however, is never a liana, and which has more or less straight filaments that are covered with unicellular hairs. *Pieris cubensis* also has calyx lobes that are densely pubescent adaxially.

The scandent habit of this species has been investigated by several botanists (Harper, 1903; Small, 1914; Lemon, 1945; Lemon & Voegel, 1962; and Hallé, Oldeman, & Tomlinson, 1978). *Pieris phillyreifolia* begins its growth on the ground, and shrubby specimens produce terete, horizontal, underground rhizomes bearing scalelike leaves with adventitious roots arising from their axils (just above the bud). These rhizomes (upon encountering a tree?) are able to ascend *Taxodium ascendens* or *Chamaecyparis thyooides* by climbing upward within the fibrous bark. (Less commonly, this species can be found climbing *Cyrilla racemiflora*, *Sabal palmetto*, or *Pinus elliotii*.) The modified climbing rhizomes are flattened and produce scale leaves. The shoot apex resembles a knifelike wedge and forces its way upward within the bark. In addition to these upward-growing rhizomes, branches are produced that break out into the air at intervals, producing normal photosynthetic leaves (see Lemon & Voegel, 1962). *Pieris phillyreifolia* may also exist as

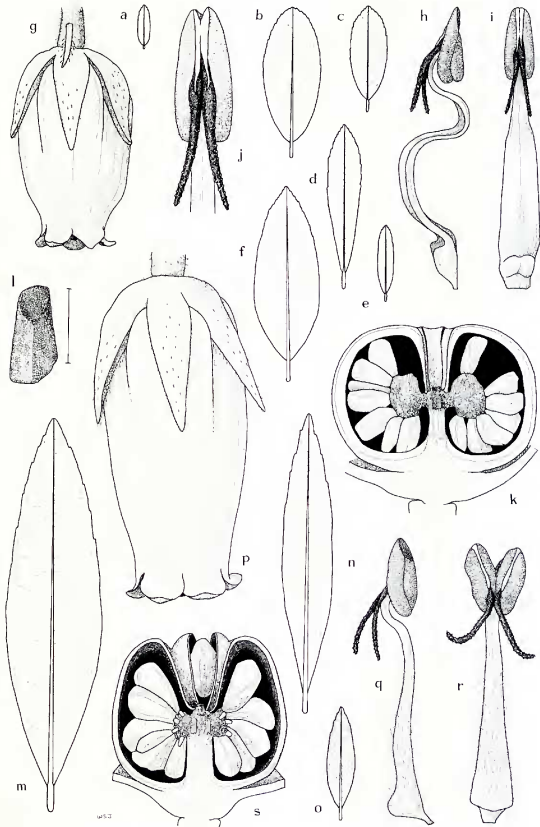
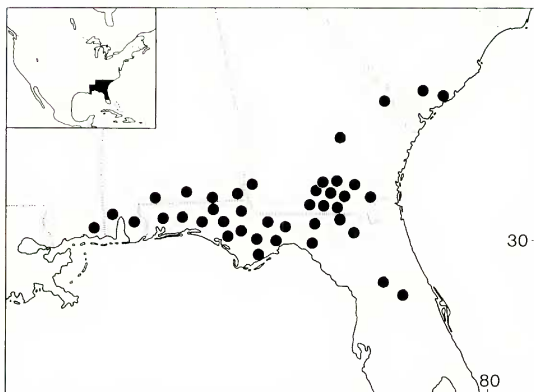


FIGURE 7. a-k, *Pieris phillyreifolia*: a-f, leaves, $\times .66$; g, flower, $\times 4$; h, i, stamens, $\times 8.5$; j, anther, $\times 17$; k, capsule, longitudinal section, $\times 8.5$; l, seed, bar = 1 mm. m-s, *P. cubensis*: m-o, leaves, $\times .66$; p, flower, $\times 4$; q, r, stamens, $\times 8.5$; s, capsule, longitudinal section, $\times 8.5$.



MAP 3. Distribution of *Pieris phillyreifolia*.

a low shrub on hummocks, old stumps, or fallen logs, or in moist openings of swamp forests.

This species is occasionally cultivated.

5. *Pieris cubensis* (Griseb.) Small, N. Am. Fl. **39**: 63. 1914.

Andromeda cubensis Griseb. Catal. Pl. Cubens. 51. 1866. TYPE: Cuba, Pinar del Río, ± La Palma, banks of rivulets, 4 July [1862], *C. Wright 2198*, in part (holotype, GOET!; isotypes, GH!, L(fragment)!, NY(3 sheets)!, S!).

Rhizomatous(?) shrub to ca. 2 m tall. Twigs terete to strongly angled with few scattered glandular-headed hairs, otherwise glabrous to sparsely pubescent. Buds ovoid to hemispheric, glabrous or with fringe of unicellular hairs along scale margins. Scales (2 or) 3 or 4, imbricate, apex rounded, acute, or slightly acuminate. Expanded leaves alternate; petiole 2–9 mm long, vascular bundle bifacial; blade elliptic to ovate or slightly obovate, 3.5–13 by 0.6–4 cm, coriaceous, the epidermis not lignified to slightly so, the apex slightly acuminate or acute to rounded, the base cuneate to attenuate, the margin plane to conspicuously revolute (especially toward base), entire except for few clear to obscure teeth near apex, the venation brochidodromous, 3° veins slightly visible and reticulate, the adaxial and abaxial surfaces with sparse glandular-headed hairs, ± glabrescent, sparsely pubescent on adaxial surface of midvein. Inflorescences axillary racemes from 1 to several buds usually near apex of branch, ± horizontal. Pedicels 2.5–7.5 mm long, with

few glandular-headed hairs, otherwise densely pubescent; bracteoles from lower 20 to upper 30% of pedicel, linear to narrowly triangular, 1–2.5 mm long; bracts 1.5–3.5 mm long, similar to bracteoles in shape. Calyx lobes elongate-triangular, acute at apex, 3–6.5 by 0.7–1.5 mm; adaxial surface densely pubescent; abaxial surface with few glandular-headed hairs, otherwise sparsely to densely pubescent. Corolla cylindrical-urceolate, weakly 5-ridged, 8–13 by 3–5 mm, white. Filaments 4–5 mm long, straight to very slightly geniculate, covered with unicellular hairs, especially near base. Style strongly impressed into apex of ovary. Capsule subglobose to short-ovoid or ovoid, 4–7 by 4.5–8 mm, glabrous or very sparsely pubescent; placentae appearing central to nearly basal with respect to capsule apex. Seeds angular-ovoid, 1.5–2 mm long, with testa composed of \pm isodiametric cells. (FIGURE 7; see also León & Alain, 1957.)

DISTRIBUTION AND ECOLOGY. Western Cuba (Pinar del Río) and Isle of Pines. (MAP 4.) Along banks of small streams (arroyos) or rivers. Flowering chiefly February to May.

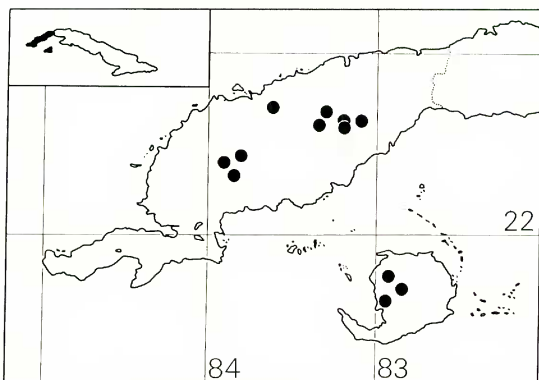
COMMON NAME. Clavellina.

REPRESENTATIVE SPECIMENS. **Cuba.** PINAR DEL RÍO: Sierra de Rangel, *Acuña* 4882 (NY); Santa Cruz de los Pinos, Valle of Taco-taco R., *Alain* 757 (GH. US); Lagunillas, Río San Sebastian, *Ekman* 13796 (s); Sierra Organos, grupo del Rosario, valley of Río Santa Cruz, *Ekman* 16387 (K, NY, s); near El Guama, *Palmer* & *Riley* 155 (NY. US); Arroyo del Sumidero, *Shafer* & *León* 13585 (NY. US); Arroyo Veintecinco, San Cristobal, Partir Palacios, *Wright* 2198, in part (GH. GOET. S). ISLA DE PINOS: vic. of Los Indios, *Britton et al.* 14240 (GH. MO. NY. S. US); S of Santa Bárbara, *Killip* 43100 (F. NY. S. US); between San Francisco de las Piedras and Cerro la Cañada, *Killip* 44617 (F. US).

Pieris cubensis is most closely related to *P. phillyreifolia*, from which it is easily distinguished by its nonclimbing habit, its more or less straight, pubescent filaments, its more sparsely toothed, often longer leaves, and its calyx lobes that are densely pubescent on the adaxial surface. Grisebach (1866), when he described this species, was aware of its close relationship to *P. phillyreifolia*. The similarities between these two species were also noticed by K. Lems (unpublished notes).

6. *Pieris swinhoei* Hemsley, Jour. Linn. Soc. Bot. **26**: 17. 1889. TYPE: China, Fukien prov., Amoy interior, June 1870, *R. Swinhoe s.n.* (holotype, K!; fragment of holotype, A!).

Rhizomatous(?) shrub or small tree to ca. 3 m tall, with brownish to gray, vertically furrowed bark. Twigs terete to slightly angled with few glandular-headed hairs, otherwise sparsely pubescent. Buds ovoid, glabrous or with few unicellular hairs along scale margins. Scales ca. 4, imbricate, apex acute to acuminate. Expanded leaves pseudoverticillate; petiole 2–7 mm long, vascular bundle unifacial; blade narrowly obovate to elliptic, (2.5–)4–12.5 by (0.4–)0.7–1.7 cm, coriaceous, the epidermis not lignified to slightly so, the apex acute, the base narrowly cuneate to attenuate, the margin revolute (es-

MAP 4. Distribution of *Pieris cubensis*.

pecially toward base), conspicuously toothed on distal half, entire or very obscurely toothed in proximal half; the venation brochidodromous, 3° veins visible and \pm reticulate, the adaxial and abaxial surfaces with sparse glandular-headed hairs, sparsely to moderately pubescent on adaxial surface of midvein. Inflorescences axillary or terminal racemes, less commonly terminal panicles with lowermost lateral branches arising from axils of uppermost foliage leaves, erect to \pm horizontal (?). Pedicels 3.5–9 mm long, with few glandular-headed hairs, otherwise moderately to densely pubescent; bracteoles from upper 15–25% of pedicel, narrowly triangular to ovate, 1.3–4 mm long; bracts 4–10 mm long, similar to bracteoles in shape, rarely approaching leaves in shape and size. Calyx lobes elongate-triangular, acute at apex, 4.5–9 by 1.2–2 mm; adaxial surface moderately to densely pubescent, especially near apex; abaxial surface with few glandular-headed hairs, otherwise glabrous or sparsely pubescent near base. Corolla cylindrical-urceolate, weakly 5-ridged, 8–10 by 3.5–5 mm, white. Filaments 5–7.5 mm long, straight to very slightly geniculate, covered with unicellular hairs, especially near base. Style strongly impressed into apex of ovary. Capsule ovoid to globose, slightly subglobose, or slightly urceolate, 3.5–4.5 by 4–4.5 mm, densely to occasionally moderately pubescent; placentae appearing central to nearly basal with respect to capsule apex. Seeds angular-ovoid, 1–1.5 mm long, with testa of \pm isodiametric cells. (FIGURE 8; see also Anonymous, 1974.)

DISTRIBUTION AND ECOLOGY. Southeastern China (Kwangtung, Fukien), Hong Kong. (MAP 1.) Rare; along stream banks. Flowering in March.

COMMON NAMES. Ma-tsui-mi, maaui-mei-fa (China).

REPRESENTATIVE SPECIMENS. **China.** KWANGTUNG: Thai-Yong, 60 mi W from Port of Swatow, *Dalziel s.n.*, 16 July 1901 (E); Taai Yeung Shaan, *McClure 535* (A); North

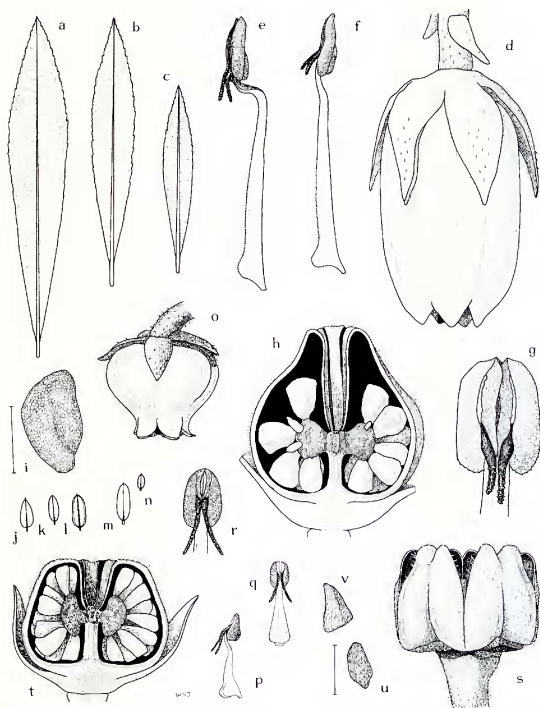


FIGURE 8. a-i, *Pieris swinhoei*: a-c, leaves, $\times .66$; d, flower, $\times 4$; e, f, stamens, $\times 8.5$; g, anther, $\times 17$; h, capsule, longitudinal section, $\times 8.5$; i, seed, bar = 1 mm. j-v, *P. nana*: j-n, leaves, $\times .66$; o, flower, $\times 4$; p, q, stamens, $\times 8.5$; r, anther, $\times 17$; s, capsule, $\times 8.5$; t, capsule, longitudinal section, $\times 8.5$; u, v, seeds, bar = 1 mm.

R., Ma Nui Pa, *McClure 1429* (A, NA, UC). **Hong Kong:** Torrent des Ligularia, Poifu-lan, *Bodinier 1407* (E).

Pieris swinhoei, a rare and little-collected species of southeastern China, is most closely related to *P. cubensis* and *P. phillyreifolia*. Like these species, it has capsules with the placentae appearing central to nearly basal with respect to the capsule apex, and seeds with more or less isodiametric testa cells. The characters best distinguishing the three species are listed in the key. *Pieris swinhoei* is easily distinguished from *P. japonica* by the above-mentioned characters, and by its larger flowers, its densely pubescent capsules, and its leaves with the secondary and prominent intersecondary veins diverging at often nearly right angles from the midvein and extending more or less straight to near the leaf margin, where they join adjacent secondary veins. In contrast, *P. japonica* has fewer and often less prominent secondary veins that diverge at more acute angles and extend more or less straight or in an upward curve toward the margin.

Pieris D. Don Subgenus **Arcterica** (Cov.) Judd, comb. nov.

Arcterica Cov. Proc. Acad. Sci. Washington **3**: 573. 1901. TYPE SPECIES: *Pieris nana* (Maxim.) Makino.

Low shrubs to ca. 10 cm tall. Twigs with homogeneous pith. Leaves usually in whorls of 3, (3-)3.5-11 mm long; margin entire. Flowers in whorls of 3 in axillary or terminal racemes. Calyx lobes often deciduous in fruit, with stomata lacking on adaxial surface; corolla 3-5 mm long; filaments 1.5-2 mm long, roughened-papillose; anthers lacking or with only poorly developed disintegration tissue on back. Capsule with placentae appearing \pm central with respect to its apex.

DISTRIBUTION. Same as species.

NUMBER OF SPECIES: 1.

7. **Pieris nana** (Maxim.) Makino, Bot. Mag. Tokyo **8**: 213. 1894.

Andromeda nana Maxim. Bull. Acad. Sci. St.-Petersb. **18**: 47. 1872. *Arcterica nana* (Maxim.) Makino, Bot. Mag. Tokyo **20**: 85. 1906. *Lyonia nana* (Maxim.) Makino, *pro. syn., ibid.* TYPE: Japan, prov. Nambu (Rikuchu), in high mountains, *Tschonoski s.n.* (holotype, LE, not seen).

Cassiope oxycoccoides A. Gray, Proc. Am. Acad. n.s. **20**: 300. 1885. *Arcterica oxycoccoides* (A. Gray) Cov. Proc. Acad. Sci. Washington **3**: 573. 1901. TYPE: Bering Island, [ca. 300 ft alt. behind fishing village of Saranna, 22 August,] 1883, *L. Steineger s.n.* (holotype, GH!).

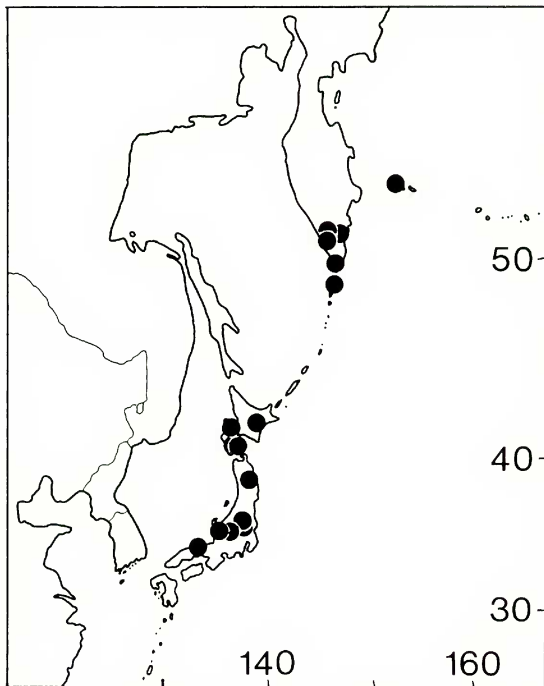
Low, rhizomatous shrub to ca. 10 cm tall. Twigs terete to slightly angled, with few glandular-headed hairs, otherwise moderately to densely pubescent. Buds flattened-ovoid, glabrous or with fringe of unicellular hairs along scale margins. Scales 3 or 4 (or 5), imbricate, apex rounded to acute. Leaves in whorls of 3, rarely opposite or alternate, scalelike and often alternate or opposite on horizontal rhizomes, alternate in seedlings; petiole 0.5-2 mm long,

vascular bundle unifacial; blade elliptic to slightly ovate, (3-)3.5-11 by 1.5-5 mm, coriaceous, the epidermis not lignified to slightly so, the apex acute to rounded, with knoblike, prominent mucro, the base rounded to very slightly cordate, the margin conspicuously revolute throughout, entire, the venation hypohydromous to brochidodromous, 2° veins obscure to slightly visible, the adaxial surface with glandular-headed hairs, otherwise sparsely pubescent (on both blade and midvein), ± glabrescent, the abaxial surface with only glandular-headed hairs. Inflorescences axillary or terminal racemes with flowers in 1 to 3 (rarely to 5) whorls of 3 flowers each, ± horizontal to pendent but becoming erect as fruits mature. Pedicels 1.5-5 mm long, with few glandular-headed hairs, otherwise densely pubescent; bracteoles from near middle to apex of pedicel, ovate, 2-3 mm long; bracts ± ovate, 2-5 mm long, often approaching leaves in shape and size. Calyx lobes triangular, acute at apex, 2.5-4 by 0.9-1.3 mm, often deciduous in fruit; adaxial surface sparsely to densely pubescent, especially near apex; abaxial surface with few glandular-headed hairs, otherwise glabrous or sparsely pubescent near base. Corolla urceolate, 3-5 by 2-5 mm, white. Filaments 1.5-2 mm long, straight, roughened-papillose, especially near base. Style strongly impressed into apex of ovary. Capsule short-ovoid or subglobose, 1.7-2.7 by 3-3.5 mm, glabrous to densely pubescent; placentae appearing ± central with respect to capsule apex. Seeds angular-ovoid, ca. 0.5 mm long, with testa of ± elongated cells. (FIGURE 8; see also Coville, 1904; Makino, 1961; Ingram, 1963.)

DISTRIBUTION AND ECOLOGY. Japan (central and northern Honshu, Hokkaido) northward to Kuril Islands, southern Kamchatka, Commander Islands (Berling Is.). (MAP 5; see also Hultén, 1930.) In Japan, ca. 1350-2700 m alt.; volcanic-rock areas, rocky peaks, exposed windswept cliffs and slopes, mountain summits, thickets, alpine scrub, dwarf-scrub heath; often with *Pinus pumila*, *Empetrum nigrum*, *Loiseleuria procumbens*, *Diapensia lapponica*, *Vaccinium uliginosum*, *Cassiope lycopodioides*, *Rhododendron camtschaticum* (see Numata, 1974). In more northern portions of range, frequently at lower elevations in low heaths or rocky windswept areas; often with mosses, lichens, *Bryanthus gmelinii*, *Loiseleuria procumbens*, *Oxytropis revoluta*, *Vaccinium vitis-idaea*. In Japan, flowering May through August (mainly July?); data insufficient to determine blooming period for other portions of range.

COMMON NAMES. Komeba-tsugazakura zoku, hama-zakura (Japan).

REPRESENTATIVE SPECIMENS. **Japan.** HOKKAIDO: Hokkaido pref., Mt. Hakamagoshi, Yamamoto s.n., 23 June 1924 (TAI), Mt. Shiribeshi, Wilson 7293 (A), Yezo, Fairie 6754 (A). NORTHERN HONSHU: Akita pref., Mt. Iwate, Furuse s.n., 27 July 1958 (A). CENTRAL HONSHU: Gumma pref., Mt. Shibutsu, Katashinamura, Nishida s.n., 17 July 1950 (A); Ishikawa pref., Mt. Hakusan, Shiota s.n., 4 Aug. 1921 (A); Nagano pref., Mt. Asama, Mizushima s.n., 17 Aug. 1951 (A), Mt. Yatsugatake, Matsuiama 2433 (A); Tochigi pref., Mt. Shirane, Mizushima s.n., 4 July 1952 (A); Tottori pref., Mt. Daisen, Wilson s.n., 30 Nov. 1914 (A).



MAP 5. Distribution of *Pieris nana*. (Distribution outside Japan based Hultén, 1930.)

Pieris nana is a very isolated taxon that is easily distinguished from all other *Pieris* species by its low habit, its small, entire-margined, usually whorled leaves, its roughened-papillose filaments, and its only poorly developed disintegration tissue. The phylogenetic isolation of this species (see Judd, 1979, and above) is expressed here by its being placed in a monotypic subgenus.

The species is occasionally cultivated.

TAXA EXCLUDED FROM PIERIS

- Pieris annamensis* Dop in Lecomte, Fl. Gén. Indo-chine **3**: 726. 1930 = **Lyonia ovalifolia** (Wallich) Drude var. **rubrovenia** (Merr.) Judd.
- Pieris bracteata* W. W. Sm. Notes Royal Bot. Gard. Edinburgh **19**: 116. 1916 = **Vaccinium sprengeii** (G. Don) Sleumer (Rehder, 1949).
- Pieris buxifolia* Lévl. Bull. Soc. Bot. France **53**: 203. 1906 = **Vaccinium triflorum** Rehder (Rehder, 1934; Chamberlain, 1977).
- Pieris cavaleriei* Lévl. & Vaniot, Bull. Soc. Bot. France **51**: 292. 1904 = **Leucothoe griffithiana** Clarke (Rehder, 1934; Chamberlain, 1977).
- Pieris chapaënsis* Dop in Lecomte, Fl. Gén. Indo-chine **3**: 726. 1930 = **Lyonia chapaënsis** (Dop) Merr.
- Pieris chapaënsis* Dop var. *glabra* Dop & Trochain, Bull. Mus. Hist. Nat. Paris II. **4**: 719. 1932 = **Lyonia chapaënsis** (Dop) Merr.
- Pieris compta* W. W. Sm. & Jeffrey, Notes Royal Bot. Gard. Edinburgh **9**: 116. 1916 = **Lyonia compta** (W. W. Sm. & Jeffrey) Hand.-Mazz.
- Pieris coreana* Lévl. Repert. Sp. Nov. **5**: 281. 1908 = **Vaccinium bracteatum** Thunb. (Rehder, 1934, 1949; Chamberlain, 1977).
- Pieris divaricata* Lévl. Bull. Acad. Géogr. Bot. **12**: 252. 1903 = **Vaccinium bracteatum** Thunb. (Rehder, 1934, 1949; Chamberlain, 1977).
- Pieris doyonensis* Hand.-Mazz. Anzeig. Akad. Wiss. Wien Math.-Naturwiss. Kl. **60**: 185. 1923 = **Lyonia ovalifolia** (Wallich) Drude var. **doyonensis** (Hand.-Mazz.) Judd.
- Pieris duclouxii* Lévl. Bull. Acad. Géogr. Bot. **12**: 253. 1903 = **Vaccinium sprengeii** (G. Don) Sleumer (Rehder, 1949; Chamberlain, 1977).
- Pieris elliptica* (Sieb. & Zucc.) Nakai, Bot. Mag. Tokyo **33**: 207. 1919. = **Lyonia ovalifolia** (Wallich) Drude var. **elliptica** (Sieb. & Zucc.) Hand.-Mazz.
- Pieris esquirolii* Lévl. & Vaniot, Bull. Soc. Bot. France **53**: 206. 1906, incl. var. **discolor** Lévl. & Vaniot = **Vaccinium sprengeii** (G. Don) Sleumer (Rehder, 1949; Chamberlain, 1977).
- Pieris fauriei* Lévl. Repert. Sp. Nov. **5**: 281. 1908 = **Vaccinium bracteatum** Thunb. (Rehder, 1934, 1949; Chamberlain, 1977).
- Pieris formosana* Komatsu in Matsumura, Ic. Pl. Koishikav. **3**: 71. t. 181. 1916 = **Lyonia ovalifolia** (Wallich) Drude var. **elliptica** (Sieb. & Zucc.) Hand.-Mazz.
- Pieris fortunati* Lévl. Bull. Soc. Bot. France **54**: 369. 1907 = **Gaultheria leucocarpa** Blume (Chamberlain, 1977).
- Pieris gagnepainiana* Lévl. Bull. Acad. Géogr. Bot. **12**: 251. 1903 = **Vaccinium fragile** Franchet (Rehder, 1934, 1949; Chamberlain, 1977).
- Pieris griffithiana* Hooker f., *pro. syn.*, Clarke in Hooker f. Fl. Brit. India **3**: 460. 1882 = **Leucothoe griffithiana** Clarke.
- Pieris henryi* Lévl. Bull. Soc. Bot. France **53**: 204. 1906 = **Lyonia ovalifolia** (Wallich) Drude var. **hebecarpa** (Franchet ex Forbes & Hemsley) Chun.
- Pieris kouyangensis* Lévl. Bull. Acad. Géogr. Bot. **12**: 253. 1903 = **Lyonia ovalifolia** (Wallich) Drude var. **lanceolata** (Wallich) Hand.-Mazz.

- Pieris lanceolata* (Wallich) D. Don, Edinburgh New Philos. Jour. **17**: 159. 1834 = **Lyonia ovalifolia** (Wallich) Drude var. **lanceolata** (Wallich) Hand.-Mazz.
- Pieris longicornu* Lévl. & Vaniot, Bull. Soc. Bot. France **51**: 291. 1904 = **Vaccinium sprengelii** (G. Don) Sleumer (Rehder, 1949; Chamberlain, 1977).
- Pieris lucida* Lévl. Bull. Soc. Bot. France **53**: 207. 1906 = **Vaccinium bracteatum** Thunb. (Chamberlain, 1977).
- Pieris macrocalyx* Anthony, Notes Royal Bot. Gard. Edinburgh **15**: 241. 1927 = **Lyonia macrocalyx** (Anthony) Airy Shaw.
- Pieris mairei* Lévl. Bull. Acad. Géogr. Bot. **25**: 21. 1915 = **Lyonia ovalifolia** (Wallich) Drude var. **hebecarpa** (Franchet ex Forbes & Hemsley) Chun.
- Pieris mariana* (L.) Benth. & Hooker, Gen. Pl. **2**: 588. 1876 = **Lyonia mariana** (L.) D. Don.
- Pieris martinii* Lévl. Bull. Acad. Géogr. Bot. **12**: 252. 1903 = **Vaccinium dunalianum** Wight var. **urophyllum** Rehder & Wilson (Rehder, 1934; Chamberlain, 1977).
- Pieris nitida* (Bartram ex Marsh.) Benth. & Hooker, Gen. Pl. **2**: 588. 1876 = **Lyonia lucida** (Lam.) K. Koch.
- Pieris obliquinervis* Merr. & Chun, Sunyatsenia **5**: 157. 1940 = **Lyonia ovalifolia** (Wallich) Drude var. **rubrovenia** (Merr.) Judd.
- Pieris oligodonta* Lévl. Bull. Soc. Bot. France **54**: 369. 1907 = **Maesa japonica** (Thunb.) Moritzi (Myrsinaceae; Lauener, 1977).
- Pieris ovalifolia* (Wallich) D. Don, Edinburgh New Philos. Jour. **17**: 159. 1834 = **Lyonia ovalifolia** (Wallich) Drude var. **ovalifolia**.
- Pieris ovalifolia* (Wallich) D. Don var. **denticulata** Lévl. Bull. Soc. Bot. France **51**: 291. 1904 = **Vaccinium bracteatum** Thunb. (Chamberlain, 1977).
- Pieris ovalifolia* (Wallich) D. Don var. **elliptica** (Sieb. & Zucc.) Rehder & Wilson in Sargent, Pl. Wilson. **1**: 552. 1913 = **Lyonia ovalifolia** (Wallich) Drude var. **elliptica** (Sieb. & Zucc.) Hand.-Mazz.
- Pieris ovalifolia* (Wallich) Drude var. **hebecarpa** Franchet ex Forbes & Hemsley, Jour. Linn. Soc. Bot. **26**: 17. 1889 = **Lyonia ovalifolia** (Wallich) Drude var. **hebecarpa** (Franchet ex Forbes & Hemsley) Chun.
- Pieris ovalifolia* (Wallich) Drude var. **lanceolata** (Wallich) Clarke in J. D. Hooker, Fl. Brit. India **3**: 461. 1882 = **Lyonia ovalifolia** (Wallich) Drude var. **lanceolata** (Wallich) Hand.-Mazz.
- Pieris ovalifolia* (Wallich) D. Don var. **pubescens** Franchet, Nouv. Arch. Mus. Hist. Nat. Paris II. **10**: 44. 1887 = **Lyonia villosa** (Wallich ex Clarke) Hand.-Mazz. var. **pubescens** (Franchet) Judd.
- Pieris ovalifolia* (Wallich) D. Don var. **tomentosa** Fang, Contr. Biol. Lab. Sci. Soc. China Bot. **10**: 241. 1938 = **Lyonia ovalifolia** (Wallich) Drude var. **lanceolata** (Wallich) Hand.-Mazz.
- Pieris pilosa* Komatsu in Matsumura, Ic. Pl. Koishikav. **3**: 73. t. 182. 1916 = **Lyonia ovalifolia** (Wallich) Drude var. **elliptica** (Sieb. & Zucc.) Hand.-Mazz.

- Pieris repens* Lévl. Bull. Acad. Géogr. Bot. **12**: 252. 1903 = **Vaccinium fragile** Franchet (Rehder, 1949; Chamberlain, 1977).
- Pieris rubrovenia* Merr. Philip. Jour. Sci. **23**: 256. 1923 = **Lyonia ovalifolia** (Wallich) Drude var. **rubrovenia** (Merr.) Judd.
- Pieris shanica* W. W. Sm. Rec. Bot. Surv. India **4**: 277. 1911 = **Craibiodendron stellatum** (Pierre) W. W. Sm.
- Pieris sinensis* Sweet, Hortus Brit. ed. 3. 439. 1839 = *Vaccinium* sp.
- Pieris ulbrichii* Lévl. Bull. Soc. Bot. France **53**: 205. 1906 = **Lyonia ovalifolia** (Wallich) Drude var. **lanceolata** (Wallich) Hand.-Mazz.
- Pieris vaccinium* Lévl. Repert. Sp. Nov. **9**: 448. 1911 = **Gaultheria leucocarpa** Blume (Chamberlain, 1977).
- Pieris villosa* Wallich ex Clarke in J. D. Hooker, Fl. Brit. India **3**: 461. 1882 = **Lyonia villosa** (Wallich ex Clarke) Hand.-Mazz.
- Pieris villosa* Wallich ex Clarke var. *pubescens* (Franchet) Rehder & Wilson in Sargent, Pl. Wilson. **1**: 554. 1913 = **Lyonia villosa** (Wallich ex Clarke) Hand.-Mazz. var. **pubescens** (Franchet) Judd.

NOMINA AMBIGUA

- Pieris compacta* W. W. Sm. in Anonymous, Ic. Corm. Sin. **3**: 174. 1974.
- Pieris langbianensis* A. Chev. ex Dop in Lecomte, Fl. Gén. Indo-chine **3**: 728. 1930. The placement of this name awaits an examination of the type.
- Pieris rolissonii* Lavallée, Arb. Segrez. 149. 1877.
- Pieris scrobiculata* Hollick, Maryland Geol. Survey, Miocene Vol. 486. fig. 1, g. 1904. A fossilized leaf of the Miocene, Calvert Formation, Prince George's Co., Maryland. Not a *Pieris*. True affinities unknown.

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